A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)

PART VI

BY

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British Museum (Natural History)

Pp. 29–119; 24 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 15 No. 2
LONDON: 1967

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 2 *of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation: *Bull. Br. Mus. nat. Hist.* (Zool.)

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 13 *January*, 1967

Price £1 15*s*.

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INTRODUCTION

THIS is the second of two papers dealing with the piscivorous species of *Haplochromis* in Lake Victoria. In the first part (Greenwood, 1962) representatives of the principal groups of piscivores were considered, and the main morphological trends within the trophic grade were discussed. The present paper covers the remaining species which have been studied to date ; undoubtedly more piscivorous *Haplochromis* species will be discovered, particularly amongst the as yet poorly sampled species of the deeper waters.

Not every species considered here is a piscivore ; those of other trophic groups are included simply because the species have the morphology of a piscivore, and presumably evolved from the same stem as their fish-eating relatives.

Also included in this paper is a species apparently endemic to the Lake Kyoga system. This step was necessary because of its close relationship with a previously undescribed species from Lake Victoria.

Some of the individual species described below, and in the previous paper, would seem to be so far removed from the generality of Victoria *Haplochromis* species as to justify their elevation to generic rank. Indeed, it could be argued that even some of the species-complexes have attained this level of differentiation. However, I do not think that the question can be dealt with until the whole Lake Victoria *Haplochromis* species-flock has been described. Even then, I doubt whether it will be possible to make any such divisions, at least generically. Perhaps a number of subgeneric groups could be justified on phyletic grounds, but these will be difficult to define. The situation closely resembles that encountered by Trewavas (1964) in the genus *Serranochromis*. However, I do not believe that her solution to the *Serranochromis* problem, the recognition of a gradal genus, is applicable to the situation amongst the piscivorous *Haplochromis* of Lake Victoria, particularly because the boundary between these species and any ancestral grade (or grades) would be even more obscure and indefinite than that separating *Serranochromis* from the *Haplochromis* of central Africa. Further complications are introduced when one considers the generic status of "*Haplochromis*" species outside Lake Victoria (and this includes the Lake Nyasa species in all their complexity) relative to the possibly polygeneric *Haplochromis* species of Lake Victoria.

Haplochromis spekii (Boulenger), 1906

(Text-fig. 1)

Pelmatochromis spekii (part) Boulenger, 1906, *Ann. Mag. nat. Hist.*, (7), **17**, 440; *Idem*, 1915, *Cat. Afr. Fish*, **3**, 416, fig. 285. (Lectotype, B.M. (N.H.), reg. no. 1906.5.30.296, and probably one paralectotype, 1906.5.30.307).

Haplochromis spekii (part): Regan, 1922, *Proc. zool. Soc. Londn.*, 179 (same specimens as above).

Haplochromis serranoides Regan, 1922, *op. cit.* (Lectotype, B.M. (N.H.) 1911.3.27.17, and probably the two paralectotypes 1904.5.19.52–3).

? *Paratilapia serranus* (part): Boulenger, 1915, *Cat. Afr. Fish*, **3**, 334 (two specimens, 1904.5.19.52–3, see above).

? *Haplochromis serranus* (part): Regan, 1922, *op. cit.* 174 (paralectotype of *P. spekii* 1904.5.30.307, see above).

LECTOTYPE: a male, 191·0 mm. S.L., from Bunjako, collected by Degen; B.M. (N.H.) reg. no. 1906.5.30.296.

NOTE ON THE SYNONYMY: Certain small specimens (those indicated above with an interrogation mark) are included in the synonymy with some uncertainty. Using the diagnostic characters currently available, small preserved specimens of *H. spekii* cannot readily be separated from similar sized specimens of *H. serranus*.

Regan (1922) distinguished *H. spekii* from *H. serranoides* on two characters: the maxillary extending to below the anterior quarter of the eye (barely reaches anterior orbital margin in *H. serranoides*), and, the caudal peduncle longer than deep (as long as deep in *H. serranoides*). Additional material shows that the difference in caudal peduncle proportions is easily masked by intraspecific variability; furthermore, I am unable to confirm the marked differences in caudal peduncle proportions which Regan found in the lectotypes of the two species. The difference in the posterior extension of the maxilla is valid for the lectotypes, but it must be noted that the jaws in *H. spekii* type are somewhat distorted because of a deformed right preorbital bone. Again, more material has shown that the maxilla has a variable posterior extension which links the extremes shown by the lectotypes of the two species.

In all other characters, including the dentition and the preserved colour patterns, the two type specimens show no trenchant differences, and I consider them to be conspecific.

Because of their small size (74 and 114 mm. S.L.) the paralectotypes of *H. serranoides* have not been included in the redescription. I think it probable that these specimens are referable to the species. A similar problem is posed by three paralectotypes of *H. spekii* (B.M. [N.H.] reg. nos. 1906.5.30.301, and 1906.5.30.297–8, of standard lengths 101·0, 91·0 and 79·0 mms. respectively). The two latter may perhaps be specimens of *H. serranus*, and the former is probably referable to *H. spekii.* However, until more is known about the characteristics of smaller specimens of *H. spekii,* I consider it inadvisable to give a definite identity to these three fishes.

DESCRIPTION : based on 44 specimens (including the lectotype of the species, and the lectotype of *H. serranoides*), 128–220 mm. standard length.

Depth of body 32·8–39·8 (mean, M = 35·6) per cent of standard length, length of head 36·1–39·3 (M = 37·4) per cent. Dorsal head profile straight, sloping at an angle of 30°–35°, the premaxillary pedicels from barely to moderately prominent and interrupting the profile.

Preorbital depth 18·0–24·2 (M = 20·7) per cent of head, least interorbital width 22·0–26·0 (M = 23·3) per cent. Snout 1·2–1·3 times as long as broad, its length in fishes $<$ 190 mm. S.L., (N = 25), 34·0–40·6 (M = 36·8) per cent of head, and in larger fishes (N = 19) 36·0–42·5 (M = 39·1) per cent. Eye diameter in fishes $<$ 200 mm. S.L. (N = 34) 17·3–22·6 (M = 20·0), and in larger individuals (N = 10) 15·7–19·4 (M = 18·0) per cent of head; ratio of eye/preorbital 0·8–1·3 (M = 1·0). Depth of cheek 25·7–32·9 (M = 29·5) per cent of head.

Caudal peduncle 16·7–19·8 (M = 17·9) per cent of standard length, 1·1–1·5 (modal range 1·2–1·3) times as long as deep.

Mouth horizontal or slightly oblique, jaws equal anteriorly or the lower projecting slightly, its length 49·2–61·3 (M = 53·8) per cent of head, 1·7–2·6 (modal range 1·9–2·1) times as long as broad. Mental symphysis smooth or with a slight protuberance. Premaxilla sometimes a little expanded medially but never beaked. Posterior tip of the maxilla reaching a point near the vertical through the anterior orbital margin or occasionally reaching this level (see also note on synonymy, p. 32).

Gill rakers: stout or moderately stout, the lower 1 to 3 reduced; 8 or 9 (rarely) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 30 (f.1), 31 (f.8), 32 (f.23), 33 (f.11) or 34 (f.1);

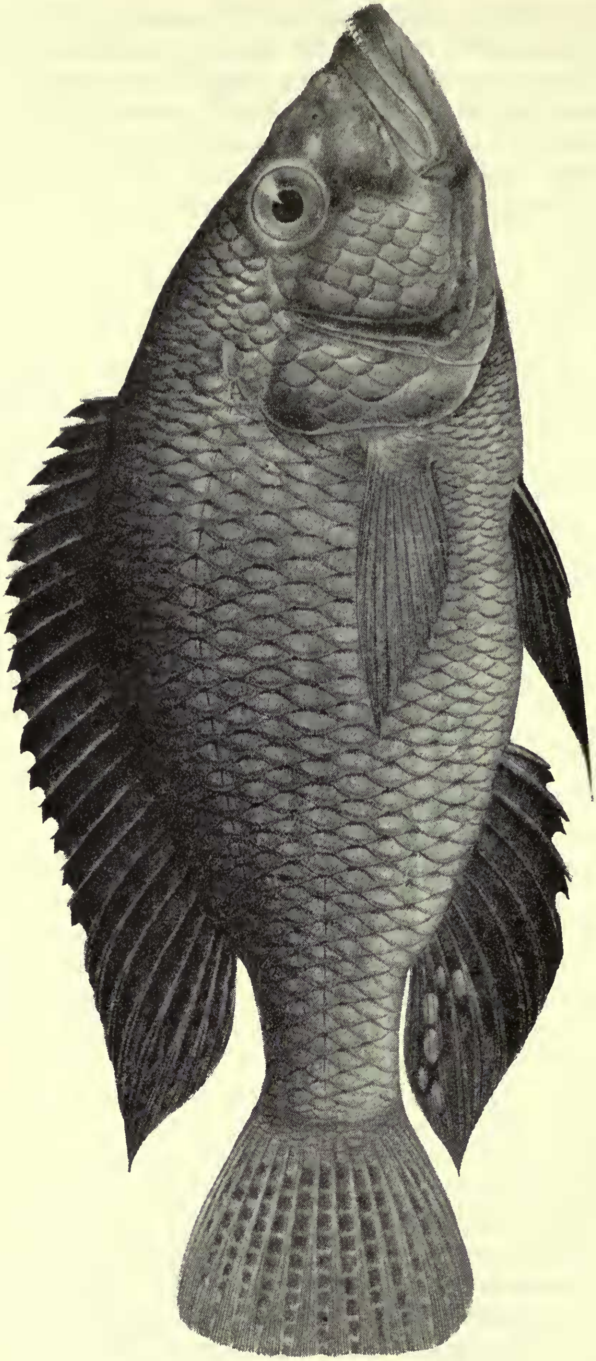

Fig. 1. *Haplochromis spekii*; lectotype; about ·77 times natural size. From Boulenger, *Fishes of the Nile*.

cheek with 3 (rare)-5 (mode 4) rows. Six to 8 (mode 7) between the upper lateral line and the dorsal fin origin, 5–9 (mode 8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.12), 25 (f.30) or 26 (f.2) rays, comprising 14 (f.1), 15 (f.29) or 16 (f.14) spinous and 8 (f.1), 9 (f.21) or 10 (f.22) branched rays. Anal with 11 (f.2), 12 (f.30) or 13 (f.9) rays, comprising 3 spinous and 8 (f.2), 9 (f.30) or 10 (f.9) branched elements. Pectoral 27·0–33·3 (M = 29·3) per cent of standard length. Pelvics with the first and second branched rays produced, slightly so in females but the first ray protracted and thread-like in males. Caudal subtruncate, scaled on its basal half.

Teeth : In all specimens examined, both the inner and outer teeth are unicuspid, those of the outer row stout and strongly curved. The smallest fish (128 mm. S.L.) shows faint indications of lateral cusps on some teeth in the inner rows.

There are 44–70 (M = 55) teeth in the outer row of the upper jaw ; inner teeth in this jaw are arranged in 3–5 (usually 3 or 4) rows, and in the lower jaw in 2 or 3 (rarely 1 or 5) rows.

Osteology. The neurocranium of *H. spekii* is identical with that of *H. serranus*, that is, of the generalized predator type showing affinity with the skull of *H. guiarti* (see Greenwood, 1962).

The lower pharyngeal bone is triangular, its dentigerous surface broader than long. The lower pharyngeal teeth are relatively fine, cylindrical in cross-section and weakly bicuspid ; some teeth are almost uniscuspid, with the larger cusp elongate and conical. The teeth are arranged in 22–24 rows.

Vertebral counts (precaudal and caudal) for six specimens are 13 + 16 (f.3), 13 + 17 (f.2) and 12 + 17 (f.1).

Coloration. Live coloration is unknown. *Preserved specimens : Males* (*adult and sexually active*) *:* Ground colour overall dusky, including the entire head, both jaws and the branchiostegal membrane ; very faint indications of a broad midlateral stripe visible behind the operculum to the beginning of the caudal peduncle where it merges with the dark general body colour. Dorsal fin dark except for the distal third to half of the soft part which is hyaline with dark spots and dashes. Caudal dark on its basal two-thirds, yellowish distally. Anal light dusky except for the distal quarter to third of the soft part which is hyaline ; 4 or 5 moderately large ocelli (dead white), usually arranged in two rows or one irregular row. Pelvic fins dusky.

Adult (*but sexually quiescent males*) have a variable ground coloration which, however, is always lighter than that of sexually active fishes. The snout and jaws are darker than the flanks which vary from dusky to light golden-brown ; branchiostegal membrane dark, but sometimes only in the region below the operculum. Dorsal fin dark, the lappets black, and the soft part often with close-set dark spots or dashes. Anal variable, from dusky to yellowish ; ocelli whiteish-grey, 2–5 in number and arranged as in active fishes. Pelvics usually dusky but of a variable intensity ; when light, the pigment concentrated over the spine and the first two branched rays.

Females (*adult and juvenile*) *:* brownish above (and on the head and snout), shading to silvery-brown or greyish-silver on the lower flanks, belly, chest and operculum ; branchiostegal membrane greyish. A faint midlateral band (of variable depth and of irregular outline) runs from behind the operculum to the caudal fin origin ; there is also a very faint upper longitudinal band running slightly above the upper lateral line visible in some specimens. All fins are brownish-yellow the soft dorsal darkly maculate. Caudal dark brown on its proximal two-thirds (because of the dense maculation in that region).

Immature males are coloured like females except that the longitudinal stripes are more distinct, and some specimens have very faint traces of 4 or 5 vertical bars crossing the longitudinal stripes on the flanks ; these bars extend from the back to a level about half way towards the ventral outline. The pelvic fins are faintly sooty.

Ecology : Habitat. Haplochromis spekii occurs over both hard and soft substrates, but seems to show a slight preference for the former. Few specimens were collected from nets operated over exposed beaches, most coming from gill-nets set in sheltered areas where the water was 10–30 ft. deep. Some specimens were taken from more exposed areas, but not from deeper water.

Food. Of the 42 fishes examined (from 24 localities), 22 contained food. Twenty-one of these had fed exclusively on small fishes (identified in 8 guts as *Haplochromis* species, in a further 8 as Cichlidae, and in one as a cyprinid). The exceptional fish contained unidentifiable fish remains and fragments of an ephemeropteran larva (probably *Povilla adusta*).

Breeding. All specimens < 150 mm. S.L. are immature, as is one specimen of 182 mm., but others > 150 mm. are mature. Both sexes reach the same maximum adult size.

Affinities. The close relationship between *H. spekii* and *H. serranus* has been noted already (see above p. 33). There is complete overlap in most characters but the differential growth trends shown by two characters are such that this overlap is considerably reduced in fishes more than 120 mm. S.L. The two characters are depth of preorbital, and eye diameter as proportions of head length. In *H. spekii* both are, generally, larger than in *H. serranus* when specimens of the same size are compared. However, even in these characters there is still some overlap, and, from the sample studied, it seems likely that neither is a reliable diagnostic character when fishes < 120 mm. S.L. are compared. The difference between *H. spekii* and *H. serranus* (in the size range 120–205 mm.) is perhaps best shown by the ratio of eye diameter to preorbital depth, *viz.*, 0·8–1·3 (mean 1·0) for *H. spekii*, and 1·1–1·5 (mean 1·3) for *H. serranus.*

Two other characters seem to show interspecific differences in their modal values. (i) In *H. serranus* the posterior tip of the maxilla usually lies below the eye or reaches to the vertical through the anterior orbital margin ; in *H. spekii* it rarely reaches as far posteriorly as the orbital margin (ii) *Haplochromis serranus* has a very prominent mental protuberance, but this bump is much weaker, if it is developed at all, in *H. spekii.* In many specimens of *H. serranus* the mental bump is so prominent that, in lateral view, the anterior margin of the dentary has a marked backward slope thus emphasizing the acuteness of the head profile ; in *H. spekii* the anterior margin of the dentary is, generally, almost perpendicular and so the tip of the head seems blunter than in *H. serranus.*

Unfortunately it is impossible to compare the live colours of adult males from the two species ; preserved coloration is similar. This information, together with more field data on niche preferences, and small specimens of *H. spekii*, will be necessary before the precise relationships (or perhaps conspecifity) of the two species can be determined. If *H. spekii* and *H. serranus* were allopatric it would be tempting, on the information available, to consider them conspecific. However, experience with other sympatric species in Lake Victoria suggests that such slight morphological differences as are known between *H. spekii* and *H. serranus* can be the only ones manifest by biologically distinct species.

Haplochromis spekii is more easily distinguished from other members of the *H. serranus* species complex.

From *H. victorianus* it is recognizable by its larger adult size (some *H. spekii* are juvenile at a size near the upper adult limits for *H. victorianus*), larger head (36·1–39·3, M = 37·4% S.L., *cf.* 33·5–36·0, M = 34·8%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 22·5–26·2, M = 24·6%), longer lower jaw, (49·2–61·3, M = 53·8% head, *cf.* 44·0–51·8, M = 47·1%), smaller eye in fishes < 200 mm. S.L. (17·3–22·6, M = 20·0% head, *cf.* 21·7–26·2, M = 24·6%), shorter pectoral fin (21·4–28·9, M = 25·1% S.L., *cf.* 26·2–32·7, M = 30·4%), and by having fewer and more curved outer teeth in the upper jaw (44–70, M = 55 teeth, *cf.* 64–86, M = 74).

From *H. maculipinna*, *H. spekii* differs in its larger adult size, longer head (36·1–39·3, M = 37·4% S.L., *cf.* 32·6–37·0, M = 35·5%), longer snout (34·0–40·6, M = 36·8% head, *cf.* 30·3–37·0, M = 33·7%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 23·2–29·8, M = 25·3%), longer lower jaw (49·2–61·3, M = 53·8% head, *cf.* 43·3–52·8, M = 48·3%), and lower eye/preorbital ratio (0·8–1·3, M = 1·0, *cf.* 1·3–1·6, M = 1·5).

Although *H. spekii* resembles *H. bartoni* a little more closely in morphometric characters than it does *H. victorianus*, the species show a greater difference in neurocranial form. The neurocrania of *H. victorianus* and *H. spekii* are virtually identical, but that of *H. bartoni* is nearest the typical " *prognathus* "-group type (see p. 109). Morphometrically, *H. spekii* differs from *H. bartoni* in having a broader interorbital region (22·0–26·0, M = 23·3% of head, *cf.* 17·0–21·0, M = 18·6%), and a somewhat smaller eye (17·3–22·6, M = 20·0% head, *cf.* 20·3–24·1, M = 22·5%). Also *H. spekii* has a lower modal number of spinous dorsal fin rays (15 *cf.* 16).

From the third member of the *H. serranus* species group, *H. nyanzae*, *H. spekii* differs in its larger adult size, larger head (36·1–39·3, M = 37·4% S.L., *cf.* 33·6–36·7, M = 35·4%), deeper cheek (25·7–32·9, M = 29·5% head, *cf.* 24·4–27·6, M = 25·9%), longer lower jaw (49·2–61·3, M = 53·8% head, *cf.* 45·0–51·6, M = 48·0%), and a lower modal number of spinous dorsal fin rays (15 *cf.* 16).

Although typical specimens of *H. spekii* and *H. gowersi* are not readily confused (compare text-fig. 1 with text fig. 13 in Greenwood, 1962) there is one specimen whose appearance is such that I am unable to place it in one species or the other ; it is even intermediate in the two quantifiable morphological characters (body depth and interorbital width) showing the greatest interspecific differences. *Haplochromis gowersi* and *H. spekii* differ markedly in neurocranial form, but without dissection this character cannot be checked with sufficient precision in the unique intermediate specimen. For the present, the possibility cannot be overruled that this fish is an interspecific hybrid.

Phyletically, *Haplochromis spekii* appears to be a derivative from an *H. serranus*-like ancestor, the principal difference between the species being the larger adult size attained by *H. spekii.*

Note : Gilchrist and Thompson (1917) record six specimens of *Pelmatochromis spekii* Blgr. from the Magalies river, Transvaal. I have not examined these specimens, but clearly they cannot be referred to *Haplochromis spekii* (Blgr.). Judging from their locality, it seems probable that they are specimens of *Chetia flaviventris* Trewavas. Dr. Trewavas is of a like opinion (personal communication).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.296 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1911.3.27.17 (Lectotype *H. serranoides*)	Victoria Nile	Melland
B.M. (N.H.) 1966.3.9.1–4, 20–21, 30–35, 39–49	Napoleon Gulf, near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.5	Beach near Nasu Point (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.11–14	Off S. tip of Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.28–29	Karenia, near Jinja (Napoleon Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.8–10	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.22	Thruston Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.27	Buka Bay (Buvuma Channel)	E.A.F.R.O.
	KENYA	
B.M. (N.H.) 1966.3.9.17–19	Kisumu (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.7	Naia Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.15–16	Sagorony (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1928.5.24.413–5	Ulambwi Bay (Kavirondo Gulf)	Graham
	TANZANIA	
B.M. (N.H.) 1966.3.9.345	Beach near Majita	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.36–38	Between Ghogororo and Isanga River	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.6	Mwanza (Capri Bay)	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.23–26	Locality unknown	E.A.F.R.O.

Haplochromis pachycephalus sp. nov.

(Text-fig. 2)

HOLOTYPE: an adult male, 199 mm. standard length, from 40 ft. of water off Kazima island, Uganda. B.M. (N.H.) reg. no. 1966.2.21.9.

DESCRIPTION: based on the holotype and fourteen other specimens 150–232 mm. standard length.

Depth of body 36·5–42·5 (M = 39·1) per cent of standard length, length of head 35·6–39·5 (M = 36·3) per cent. Dorsal head profile straight to moderately concave, the concavity exaggerated by the prominent premaxillary pedicels; nuchal region prominent and gently convex, prenuchal region sloping at 30°–35°. Cephalic lateral line pores large, especially on the preorbital and preopercular bones, less so on the dentary.

Preorbital depth 18·9–22·5 (M = 20·8) per cent of head, least interorbital width 24·6–31·3 (M = 27·8) per cent. Snout 1·1–1·4 (mode 1·2) times broader than long, its length 32·4–38·2 (M = 35·9) per cent of head; eye diameter 18·8–22·2 (M = 20·6) per cent, depth of cheek 26·4–36·1 (M = 30·8) per cent.

Caudal peduncle 13·2–16·0 (M = 14·8) per cent of standard length, 1·0–1·3 (mode 1·2) times as long as deep.

Mouth oblique, sloping at an angle of 35°–45° (mode 40°). Jaws equal anteriorly or lower projecting slightly, its length 51·5–58·4 (M = 55·0) per cent of head, 1·5–1·9 (one specimen 2·2) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior orbital margin or nearly so.

Gill rakers: stout, the lower 1 or 2 sometimes reduced, the upper 3 or 4 sometimes expanded; 8 or 9 (7 in one specimen) on the lower part of the first gill arch.

Scales ctenoid; lateral line with 32 (f.3), 33 (f.4), 34 (f.4) or 35 (f.3), cheek with 5 or 6 (rarely 4) rows. Nine or 10 (less frequently 7, 8 or 10½) between the upper lateral line and the dorsal fin origin, 7 or 8 (less frequently 6 or 9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.6), 25 (f.6) or 26 (f.1) rays comprising 15 (f.9) or 16 (f.5) spinous and 8 (f.1), 9 (f.10) or 10 (f.3) branched rays. Anal with 11 (f.2) or 12 (f.12) rays, comprising 3 spines and 8 (f.2) or 9 (f.12) branched elements. Pectoral 21·6–30·9 (M = 24·6) per cent of standard length. Pelvics with the first branched ray produced in sexually active males, slightly so in females and quiescent males.

Teeth. The outer row in both jaws is composed of unicuspid, slender and slightly curved teeth. There are 60–80 (M = 70) teeth in the outer row of the upper jaw.

Teeth in the inner rows are small, unicuspid, curved (strongly so in the upper jaw) and implanted obliquely. There are 4 or 5 (less frequently 2 or 3) rows in the upper jaw and 2 or 3 (rarely 4) in the lower.

Osteology. No complete skeleton is available. The lower pharyngeal bone is triangular, with its dentigerous surface slightly broader than long (most markedly so in the smallest fish), or rarely, as long as broad. Lower pharyngeal teeth fairly coarse, their crowns weakly cuspidate and barely compressed; some teeth in the two median rows are almost conical. The teeth are arranged in 18–22 rows.

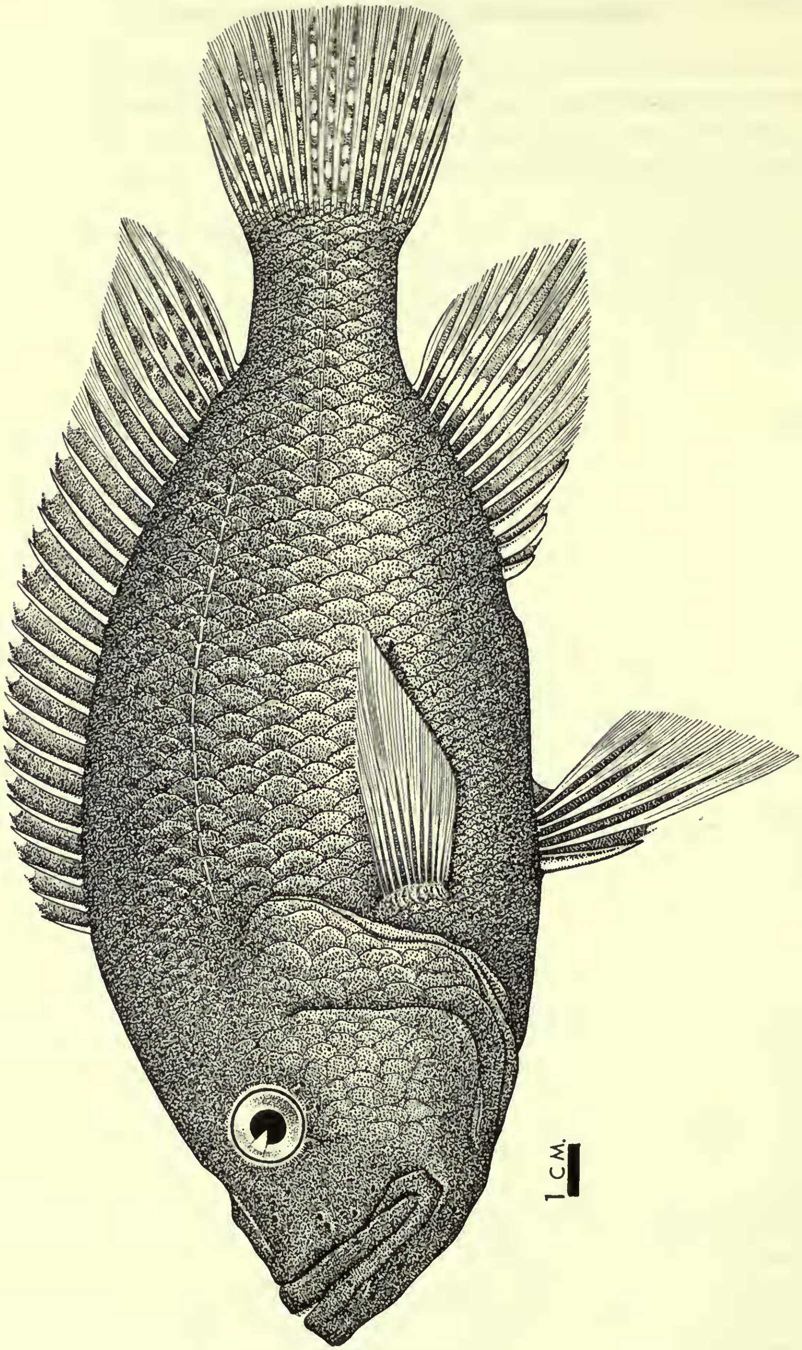

Fig. 2. *Haplochromis pachycephalus.* Drawn by Lavinia Beard.

Vertebral counts in 5 specimens are : 13 + 16 (f.3), 14 + 16 (f.1) and 14 + 17 (f.1).

Coloration : Live colours are unknown. *Preserved material : Adult males.* Ground colour variable and probably dependent on sexual state (also affected by preservation). Body greyish with black belly, chest and branchiostegal membrane, or the black replaced by a sooty-grey (in such specimens the branchiostegal membrane may be dark grey and flecked with sooty blotches) ; very faint traces of a broad midlateral stripe on the flank, originating behind the operculum and extending to the caudal fin origin. Dorsal fin greyish, dark lappets and maculae on the soft part. Caudal greyish, darkly maculate between the rays. Anal yellowish with a faintly sooty base, especially on the anterior part and around the ocelli ; the latter are dead-white, 5–9 (usually 5 or 6) in number and arranged in from 1 to 3 irregular rows. Pelvics blotched sooty to entirely black (the latter condition associated with the darkest body coloration).

Two fishes (both from the same net haul) are more sexually active than the others. Both are a very dark brown, almost uniformly so except for a black belly, chest and branchiostegal membrane. The spinous dorsal is a very dark brown (nearly black), the soft part is lighter and has a yellowish margin. Caudal light brown with lighter maculae on the basal three-quarters. Anal very faint pink, with a narrow black basal streak which expands in the region of the proximal row of ocelli and extends in amongst them ; the ocelli are whiteish.

Females (*adult but quiescent* ; based on two specimens only). Ground colour silver-grey becoming creamy on the chest and belly. Entire head (including the lower jaw) brownish with darker and irregular mottling. Body also mottled with sooty blotches, the effect being generally irregular except that on the flanks the blotches have some faint organisation into near vertical, broad bands extending from the dorsal outline to almost the ventral outline. There is some resemblance between this coloration and that of *H. cavifrons* (see Greenwood, 1962), although in *H. pachycephalus* the effect is less definitely that of freckling. Dorsal fin yellowish-grey with sooty freckling and blotching. Caudal densely and darkly blotched on its proximal third to half, greyish and darkly maculate distally. Anal greyish-yellow, with a narrow, sooty band along its base, and a duskiness over the spinous part ; both fishes have two large and distinct, dead white ocelli (an unusual feature in females). Pelvics hyaline with irregular sooty blotches.

Ecology. Habitat. The species is known from four localities ; all are some distance off-shore but close to islands. The specimens all came from nets set on a soft bottom at depths of 100–120 ft., except in one locality where the collection was made after the use of explosives. In this instance the charge was set off in about 40 ft. of water over a rock shelf with deeper water on its off-shore side.

Food. Of the 13 specimens examined (from 5 localities) six contained food in the stomach or intestines. All yielded macerated fish remains. Fragments of *Haplochromis* species were identified from three guts, a cyprinid fish in a fourth, and cichlid remains in two others.

Breeding. Little information is available about the breeding habits of *H. pachycephalus*. All specimens except the smallest (a male, 150 mm. S.L.) are mature. The two largest fishes (232 mm. and 228 mm. S.L.) are males.

Affinities. *Haplochromis pachycephalus* is, at least on superficial characters and those detectable on a radiograph, related to the *H. serranus* species group (see p. 109).

From *H. serranus*, *H. pachycephalus* is distinguished by its broader snout, broader interorbital (24·6–31·3, M = 27·8% head, *cf.* 20·4–26·8, M = 23·3%) and lower jaw (length/breadth ratio 1·5–1·9 *cf.* 1·8–2·5), and its smaller nuchal scales.

From *H. victorianus* it differs in its broader interorbital (24·6–31·3, M = 27·8% head, *cf.* 21·5–24·5, M = 22·6%), deeper cheek (26·4–36·1, M = 30·8% head *cf.* 22·5–26·2, M = 24·6%) and longer lower jaw (51·5–58·4, M = 55·0% head, *cf.* 44·0–51·8, M = 47·1%) ; the lower jaw is also broader in *H. pachycephalus.*

From *H. spekii* and *H. maculipinna*, the oblique mouth and broad snout of *H. pachycephalus* serve as immediately diagnostic characters, although the snout in *H. maculipinna* is broader than in other members of the " *serranus* "-group (being as much as 1·1 times broader than long, but generally as long as broad). As with other members of the group, *H. maculipinna* and *H. spekii* have a narrower interorbital region than *H. pachycephalus* ; *H. maculipinna* also has a larger eye (24·0–31·7, M = 26·3% head *cf.* 18·8–22·2, M = 20·6% in *H. pachycephalus*) but the larger adult size reached by *H. pachycephalus* may influence this character.

The same superficial characters (including the oblique mouth) serve to distinguish *H. pachycephalus* from *H. bartoni* and *H. nyanzae*, the former a member of the " *prognathus* " group, the latter a " *serranus* " group member.

Haplochromis boops and *H. thuragnathus* (both " *serranus* "-group species) closely resemble one another (see pp. 50) and *H. pachycephalus.* Both differ from *H. pachycephalus* in the following characters : a narrower interorbital, shorter snout, larger eye, and larger nuchal scales. All three species have the snout broader than it is long.

From the evidence available, *H. pachycephalus* would seem to be derived from an *H. serranus*-like ancestor, the principal morphological changes being an increase in mouth size coupled with greater obliquity of the mouth angle. The larger cephalic lateral line pores of *H. pachycephalus* are probably correlated with the deep water habitat of the species (as compared with *H. serranus* and its immediate allies).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.) 1966.3.9.175–177	Off S. tip of Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.174	Deep water off Dagusi Island	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.9 (Holotype)	Off Kazima Island	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.166–169, 171–173	Off Kazima Island	Uganda Fisheries Dept.
	Tanzania	
B.M. (N.H.) 1966.3.9.170	Off Godziba Island	E.A.F.R.O.
	Lake Victoria	
B.M. (N.H.) 1966.3.9.178	Locality unknown	E.A.F.R.O.

Haplochromis maculipinna (Pellegrin), 1913

(Text-fig. 3)

Paratilapia maculipinna Pellegrin, 1913 *Bull. Soc. Zool. France*, **37**, 311 ; *Idem*, 1914, in *Voyage de Ch. Alluaud et R. Jeannel en Afrique Occidental*, 16, Pl. 1, fig. 1, Paris.
Paratilapia prognatha (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333.
Haplochromis maculipinna : Regan, 1922, *Proc. zool. Soc. Londn.*, 177, fig. 5.

HOLOTYPE : a fish 122·0 mm. S.L. (Paris Museum No. 12–258) from Port Florence (Kavirondo Gulf) collected by Alluaud and Jeannel.

This specimen differs from all others now included in the species by its much larger eye. In other characters, however, it agrees with these specimens and differs from the few other Victoria *Haplochromis* species characterized by large eyes.

DESCRIPTION : based on 33 specimens (including the holotype), 91·5–166 mm. S.L.

Depth of body 33·3–37·0 (M = 35·9) per cent of standard length, length of head 32·6–37·0 (M = 35·5) per cent. Dorsal head profile straight or slightly concave in those fishes with prominent premaxillary pedicels, sloping at 30°–35°.

Preorbital depth 16·4–20·4 (M = 18·2) per cent of head, least interorbital width 20·7–25·5 (M = 22·8) per cent. Snout as long as broad to 1·1 times broader than long, its length 30·3–37·0 (M = 33·7) per cent of head, eye diameter 24·0–29·2 (31·7 in the type), mean 26·3 per cent, ratio of eye/preorbital 1·3–1·6 (M = 1·5) but 1·9 in the type ; depth of cheek 23·2–29·8 (M = 25·3) per cent.

Caudal peduncle 14·5–18·8 (M = 16·3) per cent of standard length, 1·2–1·8 (modal range 1·2–1·5) times as long as deep.

Mouth moderately oblique, sloping upwards at 35°–40°, lower jaw projecting slightly to strongly, its length 43·3–52·8 (M = 48·0) per cent of head, 1·6–2·3 (modal

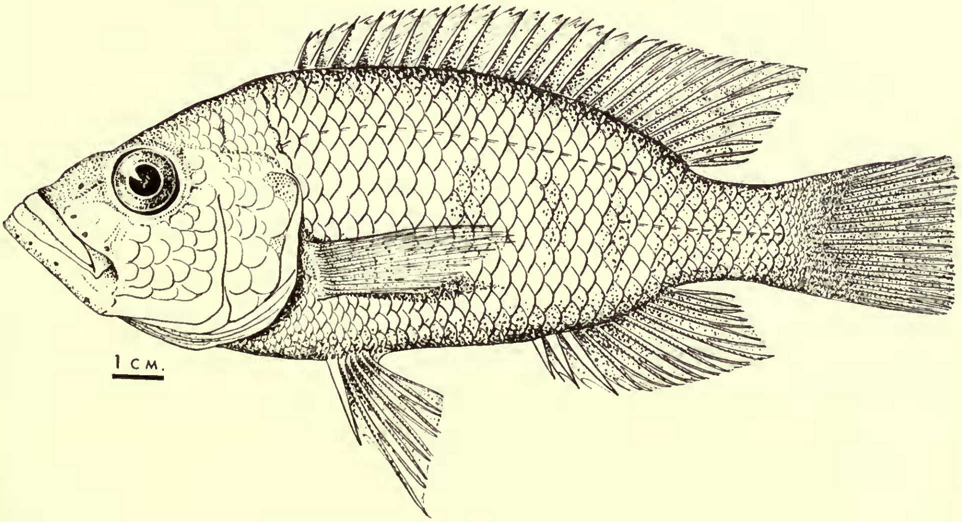

FIG. 3. *Haplochromis maculipinna.* Drawn by Barbara Williams.

range 1·7–2·1) times as long as broad. Lips not noticeably thickened, premaxilla not expanded medially. Posteriorly tip of the maxilla not quite reaching the vertical through the anterior orbital margin.

Gill rakers : moderately stout, the lower 1–3 reduced, the upper 2–5 flat and sometimes divided ; 8–11 (mode 10) on the lower part of the first arch.

Scales : ctenoid ; lateral line with 31 (f.1), 32 (f.15), 33 (f.15) or 34 (f.2), cheek with 3–5 (mode 3) rows. Five and a half (rare) to 8 (modal range 6–7) scales between the upper lateral line and the dorsal fin origin, 5½ (rare)–9 (modal range 7–8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.5), 25 (f.26) or 26 (f.2) rays, comprising 14 (f.1), 15 (f.24) or 16 (f.8) spinous and 9 (f.11) or 10 (f.22) branched rays. Anal with 11 (f.3), 12 (f.27) or 13 (f.3) rays, comprising 3 spines and 11 (f.3), 12 (f.27) or 13 (f.3) branched elements. Pectoral 23·0–31·0 (M = 26·4) per cent of standard length. Pelvics with the first two branched rays produced in both sexes, but markedly elongate in adult males. Caudal truncate to subtruncate.

Teeth. Except in the smallest specimen (91·5 mm. S.L.), the outer teeth are unicuspid ; in the exceptional fish most teeth are weakly bicuspid but a few are unicuspids. All outer teeth are slightly curved and slender, the curvature being most marked in teeth situated laterally and posterolaterally ; teeth situated posterolaterally in the upper jaw are the smallest and finest. There are 50–80 (M = 62) teeth in the outer row of the upper jaw.

Teeth in the inner rows are more variable in form, and there is no clear-cut correlation between tooth form and the fish's size. The smallest specimen has only tricuspid inner teeth ; other and larger fishes may have only weakly tricuspids in both jaws, or tricuspid teeth predominating in both jaws but some unicuspids occurring in the lower jaw, or an admixture of tri- and unicuspids (the latter predominating) in the upper jaw and only unicuspids in the lower, or a mixture of tri- and unicuspids in both jaws, or unicuspids in the upper jaw and an admixture in the lower, or only unicuspids in both jaws. Some of the largest fishes fall in either the mixed uni- and tricuspid category or in the purely unicuspid one.

The inner teeth are arranged in 1 (rare)—4 (modes 2 and 3) rows in the upper jaw, and 2 (less commonly 1 or 3) rows in the lower.

Osteology. The neurocranium of *H. maculipinna* is virtually identical with that of *H. serranus*, differing only in having a relatively lower supraoccipital crest. The premaxilla, dentary and suspensorium are also like those of *H. serranus*, except that the dentary is somewhat deeper and shorter in *H. maculipinna*.

The lower pharyngeal bone is triangular and rather fine ; the dentigerous surface is slightly broader than long. Lower pharyngeal teeth are slender and distinctly cuspidate, those of the two median rows are the coarsest ; the teeth are arranged in 20–24 rows.

Vertebral counts for seven specimens are : 13 + 16 (f.1) ; 13 + 17 (f.3) ; 14 + 16 (f.2) and 14 + 17 (f.1), giving totals of 29 to 31.

Coloration : Live colours are unknown. *Preserved specimens : Males* (*adult and sexually active*) : ground colour very dark brown, almost black, with a golden underlay on the flanks and operculum, and a sooty overlay on the chest. Head, including the lower jaw, dark but lips light brown. A very faint, but broad, lachrymal stripe runs from the antroventral margin of the orbit to the angle of the lower jaw. The branchiostegal membrane is black. Dorsal fin almost uniformly dark sooty, the lappets black. Caudal dark on its proximal three-quarters, dusky distally. Anal dusky, but with a black band along its base, the band expanding anteriorly to cover most of the spinous part of the fin, which is black ; two or three large greyish ocelli are present. Pelvics black to dusky.

Males (*adult but sexually quiescent*) *:* ground colour dark golden brown, lightest on the anterior flanks. Head dark brown, with a distinct, narrow lachrymal stripe from orbit to angle of lower jaw, and a narrow black vertical bar on the ascending preopercular limb ; branchiostegal membrane greyish-brown. Dorsal fin yellowish-grey, with black lappets, and the membrane between the branched rays dark grey-brown ; the pigment often broken into discrete maculae between the last three or four branched rays. Caudal dark yellowish-grey. Anal uniformly yellowish, with two or three faint, whiteish ocelli. Pelvics dark on the anterior third, otherwise yellowish to hyaline.

Males (*immature*) *:* ground colour light brown on the flanks and belly, darker above the upper lateral line and on the dorsum of the head ; the branchiostegal membrane is light brown-grey, and a faint lachrymal stripe is visible. On the flanks there is a trace of an interrupted, dark midlateral band on the anterior half of the body, and a continuous band on the posterior half, extending to the caudal origin. Dorsal fin yellowish-brown, the lappets dark, as are the maculae between the branched rays. Caudal yellowish-brown, with dark elongate blotches between the rays. Anal uniformly yellowish-brown, with two or three, distinct and dusky-grey ocelli. Pelvics yellowish with a faint dusky overlay, especially over the anterior part of the fin.

Females (*adult and juvenile*) *:* ground colour golden brown, darker on the upper half of the body, and the dorsal surface of the head ; faint traces of a rather broad lachrymal stripe are often visible, the stripe generally not extending to below the level of the maxilla, but reaching the angle of the lower jaw in some specimens. Faint traces of an interrupted midlateral band on the anterior half of the body, and a continuous band on the posterior half are often visible ; in some specimens no lateral band is visible, and in others the band is continuous except for a short break at about its midpoint. A few specimens show indications of a much interrupted band (really a series of 6 or 7 broad blotches) running slightly above the upper lateral line on the anterior half of the flanks, and on the lateral line posteriorly. Dorsal fin yellowish, usually darker between the posterior spines, and darkly maculate on the soft part, but uniformly yellowish with very faint maculations posteriorly in others. Anal, caudal and pelvic fins uniformly yellowish.

Ecology. Although some individuals occur over sandy, exposed and wave-washed beaches, members of this species are commoner in sheltered gulfs and bays where the water is from 10–30 ft. deep and the substrate is either soft mud or sand and shingle ; a few specimens are from deeper water (35–40 ft.) near off-shore islands.

Food. Eleven of the 30 specimens examined (from 16 localities) contained food in the stomach and intestines. Seven fishes yielded fragmentary fish remains (identified as a cyprinid in one, and as *Haplochromis* species in two others), three contained fragmentary insect remains (probably larval Ephemeroptera), and one bottom debris.

Breeding. Little information is available; most specimens less than 140 mm. S.L. are immature, as is one slightly larger individual (145 mm.). Both sexes attain the same maximum adult size.

Affinities. In both its gross and detailed morphology *H. maculipinna* shows affinity with the "*serranus*" species group, i.e. *H. serranus*, *H. victorianus*, *H. spekii*, and their deep water relatives *H. pachycephalus*, *H. boops* and *H. thuragnathus*. Criteria for distinguishing *H. maculipinna* from all but the first two species are considered under the descriptions of those species (see pp. 37, 42, 49 and 51 for the species respectively).

From *H. serranus*, *H. maculipinna* is distinguished by its larger eye (24·0–31·7, M = 26·3% head, *cf.* 20·4–26·0, M = 23·3%), shorter and more oblique lower jaw (43·3–52·8, M = 48·3% head, *cf.* 47·7–60·0, M = 54·3%), and higher eye/preorbital ratio (1·3–1·6, M = 1·5 *cf.* 1·1–1·5, M = 1·3).

From *H. victorianus*, it differs in its larger eye (24·0–31·7, M = 26·3% head *cf.* 21·7–25·5 M = 23·6%), higher eye/preorbital ratio (1·3–1·6, M = 1·5, *cf.* 1·1–1·3, M = 1·2), more oblique lower jaw (sloping at 30°–35° *cf.* horizontal or very slightly oblique) and its fewer and finer outer teeth (50–80, M = 62, *cf.* 64–86, M = 74 teeth in the upper jaw).

The close resemblance between *H. maculipinna* and these two species is obvious, and is greater than the resemblance between *H. maculipinna* and other members of the "*serranus*" group.

There are two other species, *H. nyanzae* and *H. bartoni* which, at least superficially, resemble members of the "*serranus*" group although *H. bartoni* seems to belong to a different phyletic line (see p. 109).

Haplochromis maculipinna differs from *H. nyanzae* in its larger eye (24·0–31·7, M = 26·3% head, *cf.* 19·1–24·0, M = 22·1%) and higher eye/preorbital ratio (1·3–1·6, M = 1·5, *cf.* 1·1–1·3, M = 1·2), and by its finer and less curved outer teeth.

From *H. bartoni*, it differs in having a shorter head (32·6–37·0, M = 35·5% standard length, *cf.* 36·2–39·7, M = 37·5%), broader interorbital (20·7–25·5, M = 22·8% head, *cf.* 17·0–21·0, M = 18·6%) and shorter, more oblique lower jaw (43·3–52·8, M = 48·3% head, *cf.* 50·8–57·0, M = 52·5%). Neurocranial form differs in the two species, that of *H. maculipinna* being of the "*serranus*" type, and that of *H. bartoni* being of the "*prognathus*" type (see p. 110).

Resemblances between *H. maculipinna* and *H. acidens* are discussed on p. 76. It seems unlikely that the species are closely related.

Phyletically, *H. maculipinna* was probably derived from a *H. serranus*-like ancestor.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.263	Bunjako	Degen
B.M. (N.H.) 1966.3.9.145–151	Napoleon Gulf, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.132–134	Beach near Nasu Point (Buvuma channel) . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.135–144	Near Ramafuta Island (Buvuma Channel) . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.129–131	Between Yempita and Busiri Island (Buvuma Channel) .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9. 124–6	Buka Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.123	Fielding Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.128	Kazima Island (near Entebbe) .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.127	Pilkington Bay	E.A.F.R.O.
	KENYA	
Paris Museum 12–258 (Holotype)	Port Florence (Kavirondo Gulf) .	Alluaud & Jeannel
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.122	Locality unknown . . .	E.A.F.R.O.

Haplochromis boops sp. nov.

(Text-fig. 4)

HOLOTYPE : an adult male, 190 mm. standard length, from 120 ft. of water, off the southern tip of Buvuma island (Uganda). B.M. (N.H.) reg. no. 1966.2.21.7.

DESCRIPTION : based on three specimens, 179–194 mm. standard length ; all are males.

Depth of body 40·5–42·3 per cent of standard length, length of head 35·3–36·1 per cent. Dorsal head profile straight, sloping steeply at 40°–50° ; premaxillary pedicels not prominent. Cephalic lateral line pores enlarged, especially those on the preoperculum, preorbital and dentary.

Preorbital depth 17·8–18·6 per cent of head, least interorbital width 21·7–25·7 per cent. Snout 1·2–1·3 times as broad as long, its length 32·6–32·8 per cent of head ; diameter of eye 23·9–25·7, depth of cheek 28·0–30·0 per cent.

Caudal peduncle 14·8–15·6 per cent of standard length, 1·2 times as long as deep.

Mouth somewhat oblique, sloping at 30°–35° (a horizontal line drawn through the tip of the lower jaw passes below the orbit). Jaws equal anteriorly or the lower projecting slightly, its length 50·0–52·5 per cent of head, 1·5–1·8 times as long as broad. Posterior tip of the maxilla reaching to a point below the anterior part of the eye.

Gill rakers : variable in form, from slender to stout, even in one individual ; the upper 3 rakers branched in one fish. Eight or 9 on the lower part of the first gill arch.

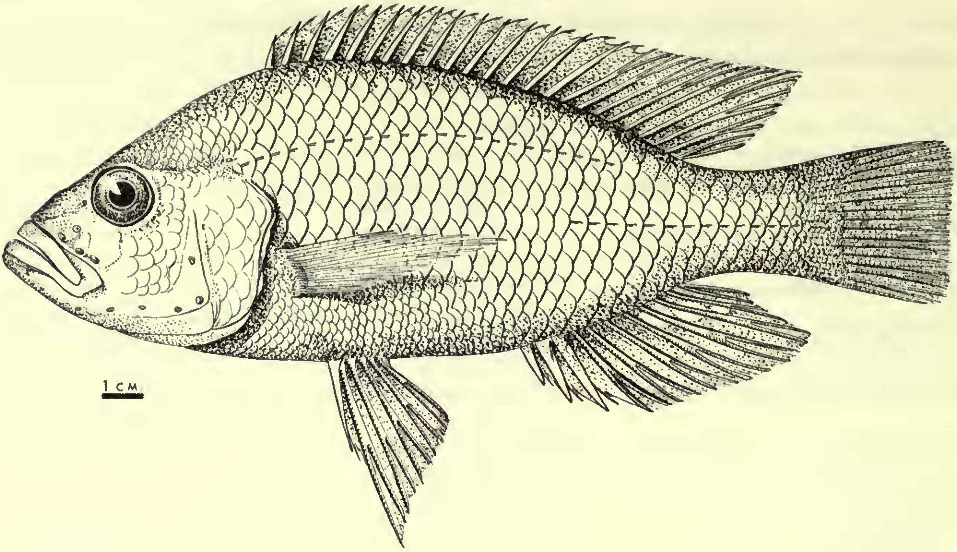

FIG. 4. *Haplochromis boops.* Drawn by Barbara Williams

Scales : ctenoid ; lateral line with 33 (f.2) or 34 scales, cheek with 4 (f.2) or 5 rows. Seven or 8 scales between the dorsal fin origin and the upper lateral line, 7 or 8 between the pectoral and pelvic fin bases.

Fins : Dorsal with 15 spines and 9 (f.1) or 10 (f.2) branched rays, anal with 3 spines and 8 (f.1) or 9 (f.2) branched rays. Pectoral 25·2–32·6 per cent of standard length. Pelvics with the first branched ray produced. Caudal subtruncate.

Teeth : In the outer row of both jaws, the teeth are small, curved and slender, with about 70 in the upper jaw.

Inner teeth, arranged in three rows in both jaws, are unicuspid, small and slightly curved.

Osteology. No complete skeleton is available, but radiographs have been studied. The lower pharyngeal bone is triangular, with its dentigerous surface broader than long. Lower pharyngeal teeth are relatively stout with cylindrical necks, and compressed, weakly cuspidate crowns. The teeth are arranged in 20–22 irregular rows. The vertebral counts in three specimens are : 13 + 16 (f.1) and 13 + 17 (f.2).

Coloration : Live colours are unknown. *Preserved material : Males (adult and sexually active) :* ground colour almost uniformly black (including the head, snout, branchiostegal membrane and belly) but with a brownish tinge. Dorsal with the spinous part blotched black on dark grey (black predominating), soft part black but with a hyaline band originating at the level of the tip of the last spine thence passing slightly downwards to end at a point about one third of the distance from the tip of the last branched ray ; the dark band distal to the hyaline strip is less intense than that along the basal part of the fin. Anal black over the spines and along the basal third of the whole fin, remainder sooty ; the five grey-white ocelli are arranged in two rows. Pelvic fins black.

No female specimens are available.

Ecology. Habitat. The two localities from which *H. boops* is known are in deep water (about 120 ft.) near islands and over mud substrates.

Food. Two specimens provided data on feeding habits. In both, the stomach had been everted, but fragments of macerated fish were collected from the pharynx and amongst the folds of the stomach wall. Judging from the scales and fin spines collected in this way, the fishes had fed on *Haplochromis*.

Breeding. All three specimens are adult, sexually active males.

Affinities. *Haplochromis boops* most closely resembles *H. thuragnathus* ; at present the species can only be distinguished by the more oblique jaw of the latter (see p. 51).

Like *H. thuragnathus*, *H. boops* appears to be a derivative of the *H. serranus* species group, probably from an ancestor resembling *H. maculipinna*. From that species *H. boops* is immediately distinguished by its broader snout (broader than long, *cf.* as long as broad), enlarged cephalic lateral line pores, and deeper body.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.) 1966.3.9.182	Near Dagusi Island . . .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.7 (Holotype)	Off southern tip of Buvuma Island	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.181	Off southern tip of Buvuma Island	E.A.F.R.O.

Haplochromis thuragnathus sp. nov.

Holotype : an adult male, 191 mm. standard length, from 120 ft. of water off the southern end of Buvuma island (Uganda) ; B.M. (N.H.) reg. no. 1966.2.21.8.

Description : based on three specimens, 191 and 200 mm. standard length. Since so few specimens are available, only ranges for morphometric characters are given.

Depth of body 39·8–41·5 per cent of standard length, length of head 34·5–35·1 per cent. Dorsal head profile slightly concave, sloping at about 30°. Cephalic lateral line pores are enlarged, especially those on the preorbital and preopercular bones.

Preorbital depth 16·4–18·8 per cent of head, least interorbital width 23·2–24·5 per cent. Snout 1·2–1·3 times as broad as long, its length 30·9–31·8 per cent of head, eye diameter 24·6–26·8, depth of cheek 27·4–29·8 per cent.

Caudal peduncle 16·0–17.7 per cent of standard length, 1·3–1·4 times as long as deep.

Mouth oblique, sloping at 40°–45°, the jaws equal anteriorly or the lower projecting slightly, length of lower jaw 53·6–56·5 per cent of head, 1·7–2·2 times as long as broad. Posterior tip of the maxilla extending to the vertical through the anterior orbital margin or to below the anterior part of the eye. A horizontal drawn anteroposteriorly through the tip of the lower jaw passes through the lower part of the eye (*cf. H. boops* where the line passes below the orbit.)

Gill rakers : stout, 9 on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 32, 33 or 34 scales, cheek with 2–4 rows. Seven or 7½ scales between the upper lateral line and the dorsal fin origin, 7 between the pectoral and pelvic fin bases.

Fins. Dorsal with 16 spines and 9 branched rays. Anal with 3 spines and 8 branched rays. Pectoral 26·0–30·0 per cent of standard length. Pelvics with the first branched ray produced, proportionately more so in males. Caudal subtruncate.

Teeth. In the outer row of both jaws, the teeth are unicuspid, small and curved ; there are 70 teeth in the upper jaw.

Inner teeth are unicuspid, small and slightly curved, and are arranged in 3 series in the upper jaw, and 2 or 3 series in the lower.

Osteology. No complete skeleton is available, but radiographs of the three specimens were examined. The lower pharyngeal bone is triangular, its dentigerous surface broader than long. The pharyngeal teeth are relatively coarse, with cylindrical necks and compressed, weakly biscuspid crowns, and are arranged in 20–22 irregular rows. Vertebral counts for all three specimens are : 13 + 17.

Coloration : Live colours are unknown. *Preserved material : Males* (*adult and sexually active*) *:* ground colour sooty over dark brown dorsally (including the head), silvery on the belly and midflank ; chest and belly darker (*i.e.* sootier), almost black There is a faint golden flush on the operculum, but it is confined to the centre of this bone and is outlined with a broad dark margin. On the flank of the lighter coloured fish are traces of a broad, dark midlateral stripe. The branchiostegal membrane is black except for its posterior and ventral margins which are greyish. Dorsal fin black except for the distal half of the soft part which is greyish. Caudal dark, but lighter towards the distal margin. Anal black on its basal half and over the spinous portion ; one large white ocellus is present in the fish with the smaller testes, but the other has 8 ocelli arranged in two irregular rows. Pelvic fins black.

Female (*quiescent*) *:* ground colour brownish, darker on back, head and snout, lighter (with silvery background) on flanks and belly ; very faint traces of a broad (three scale rows deep) interrupted midlateral band on the flanks. Operculum silvery ; a faint, dark lachrymal stripe from the orbit to behind the posterior tip of the maxilla. All fins grey-brown, the anal with 3 small, whiteish spots in the position occupied by the ocelli in males ; pelvics more grey than brown.

Ecology. Habitat. All three specimens came from nets set on the mud-bottom in water about 120 ft. deep off the southern tip of Buvuma island.

Food. Two of the three specimens examined had fragments of small *Haplochromis* species in the stomach and intestines ; the guts of the third fish were empty.

Breeding. The three specimens are adults, the two males sexually active, the female quiescent.

Affinities. Haplochromis thuragnathus is most closely related to *H. boops.* Indeed, when more material is available it may be shown that the species are not distinct. Information on the live coloration of adult males of the two species would be extremely useful in establishing their status. From *H. boops, H. thuragnathus* is distinguished by its more oblique lower jaw. If a horizontal line is drawn posteriorly from the tip of the lower jaw (when closed) it passes through the lower part of the eye in *H. thuragnathus*, but below the eye in *H. boops*.

A third member of this group, *H. pachycephalus*, is compared with *H. thuragnathus*. on p. 42.

It seems probable that *H. thuragnathus* was derived from an *H. maculipinna*-like ancestor, and more particularly from one like *H. boops* (assuming that the more oblique lower jaw is a derived condition). Like *H. pachycephalus* and *H. boops*, *Haplochromis thuragnathus* differs from other members of the "*serranus*" phyletic assemblage by its broad snout, and from individual members of the group by various combinations of morphometric characters (see descriptions of *H. serranus* and *H. victorianus* in Greenwood, 1962, and of *H. maculipinna* and *H. spekii* on pp. 46 and 37 above).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.2.21.8	Off S. tip of Ramafuta Island .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.179–180	Off S. tip of Ramafuta Island .	E.A.F.R.O.

Haplochromis xenostoma Regan, 1922

(Text-figs. 5 and 6)

Paratilapia prognatha (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333 (two specimens, one collected by Sir H. H. Johnston, the other from Entebbe and collected by Degen).

Haplochromis xenostoma, Regan, 1922, *Proc. zool. Soc. Londn.*, 185, fig. 10.

LECTOTYPE: an immature fish 104·0 mm. S.L. (B.M. [N.H.]reg. no. 1901.6.24.90) collected by Sir H. H. Johnston from Lake Victoria (locality unspecified).

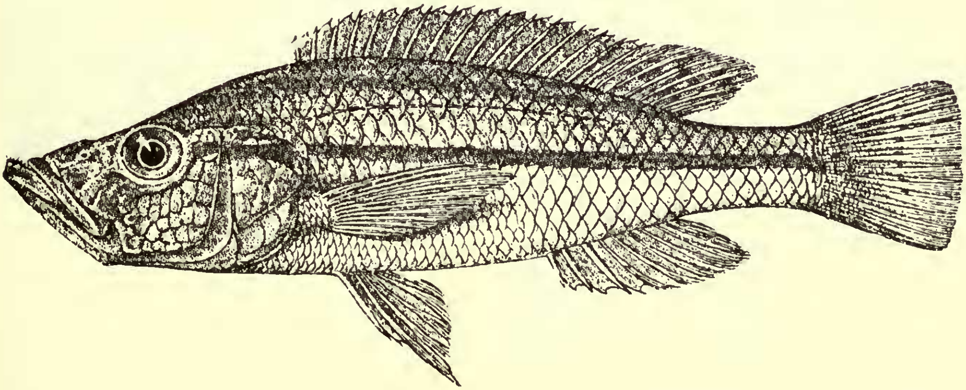

FIG. 5. *Haplochromis xenostoma*, juvenile; lectotype, about natural size. From Regan, *Proc. zool. Soc.*

DESCRIPTION : based on 27 specimens (including the lectotype) 99–203 mm. S.L. but excluding the paralectotype. Only four specimens are less than 140 mm. S.L. (99, 104 [lectotype], 106 and 119 mm. respectively) ; on the basis of this material it appears that body depth and lower jaw length may show some slight positive allometry.

Depth of body 27·0–40·0 (M = 36·5) per cent of standard length, head length 34·6–39·7 (M = 37·3) per cent. Dorsal head profile straight or slightly convex, sloping at an angle of 20°–30°, its outline noticeably interrupted by the prominent premaxillary pedicels which give it a stepped appearance.

Preorbital depth 17·5–22·7 (M = 20·3) per cent of head, least interorbital width 20·4–27·5 (M = 24·5) per cent. Snout 1·2–1·5 times as long as broad, its length 34·2–39·2 (M = 37·4) per cent of head ; eye diameter 18·5–24·3 (M = 19·7), depth of cheek 24·3–30·8 (M = 28·1) per cent.

Caudal peduncle 14·3–18·3 (M = 15·3) per cent of standard length, 1·1–1·7 (modal range 1·3–1·4) times as long as deep ; the lectotype has an unusually shallow peduncle (ratio 1·7).

Mouth very oblique, sloping at an angle of 40°–45°, the lower jaw strongly projecting beyond the upper, its length 50·0–62·0 (M = 57·0) per cent of head and 2·0 (rarely)–3·0 times as long as broad (modal range 2·3–2·5). Posterior tip of maxilla generally not reaching the vertical through the anterior orbital margin, but reaching this point in a few specimens.

Gill rakers : short and stout, or relatively slender and elongate, the lower one or two reduced ; 8–10 (mode 9) on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 29 (f.1), 31 (f.10), 32 (f.12), 33 (f.3) or 34 (f.1), cheek with 3 (mode) or 4 rows. Six or 7 (rarely 5 or 8) scales between the upper

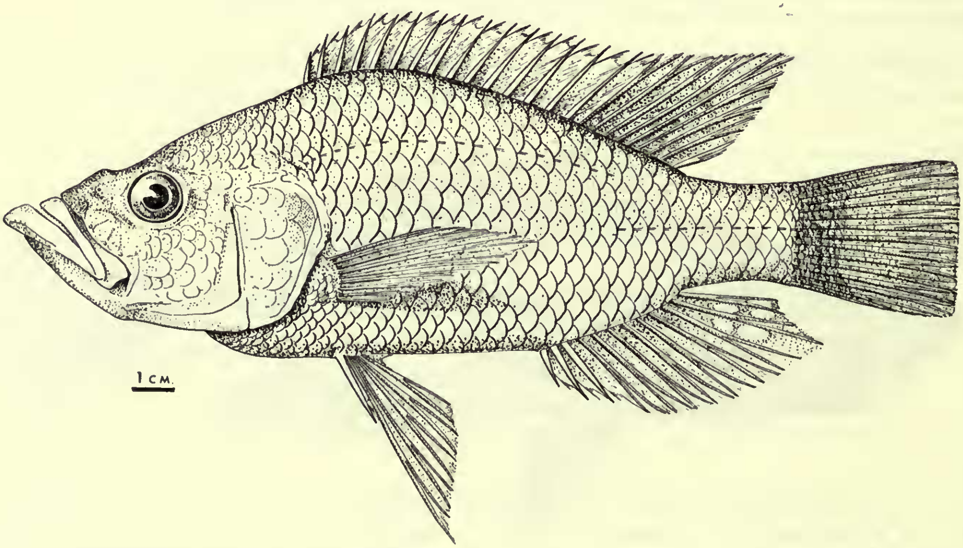

FIG. 6. *Haplochromis xenostoma* adult. Drawn by Barbara Williams.

lateral line and the dorsal fin origin, 5–7 (rarely 8) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.9), 25 (f.17) or 26 (f.1) rays, comprising 14 (f.1), 15 (f.22) or 16 (f.4) spinous and 9 (f.11) or 10 (f.16) branched rays. Anal with 11 (f.11) or 12 (f.16) rays, comprising 3 spines and 8 or 9 branched elements. Pelvics with the first two branched rays produced in both sexes but proportionately more so in adult males. Pectoral 24·2–33·0 (M = 28·0) per cent of standard length. Caudal truncate, scaled on its proximal half or slightly more.

Teeth. In fishes 119 mm. S.L. and above, the outer teeth in both jaws are unicuspid and moderately stout (but occasionally slender), those in the anterior part of the jaw with a slight inward curvature, and those situated laterally and posteriorly even less curved. The lectotype (104 mm. S.L.) has an outer dentition like that of larger fishes, but in the other small fishes (88–106 mm. S.L.) the outer teeth are distinctly bicuspid anteriorly, and weakly bicuspid laterally and posterolaterally. There are 56–94 (M = 82) teeth in the outer row of the upper jaw.

Fishes less than 106 mm. S.L. have either only tricuspid teeth or a mixture of uni- and tricuspids (some weakly so) in the inner series. A specimen 119 mm. S.L. has predominantly bicuspid teeth in the upper jaw, but in the lower jaw the first row of inner teeth is composed of unicuspids, and the other rows of tri- and weakly tricuspids. In all other specimens the inner rows are composed entirely of unicuspids. Inner teeth may be implanted somewhat obliquely so as to be medially inclined. The teeth in the outermost row of the upper inner series are often noticeably larger than their congeners. There are 2–5 rows of inner teeth in the upper jaw, and 2 or 3 (rarely 4) in the lower.

Osteology. The neurocranium of *H. xenostoma* is similar to that of *H. victorianus* (see Greenwood, 1962) but has a longer preorbital face (30·3 per cent of neurocranial length *cf.* 26·0 per cent ; the preorbital face being measured from the anterior tip of the vomer to the lateral ethmoid) ; the neurocrania of the two species also differ in that the supraocciptal crest of *H. xenostoma* is relatively higher and more pointed than in *H. victorianus*. It differs from the neurocranium of *H. serranus* (as it does from that of *H. victorianus*) in its less curved dorsal profile, and its longer preorbital face.

The very oblique and prognathous lower jaw is reflected in certain details of the suspensorium (text-fig. 7) ; all comparisons were made with *H. serranus*, a species

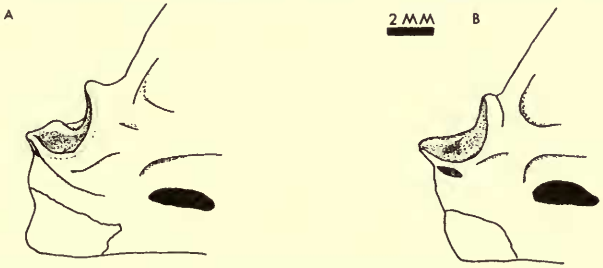

FIG. 7. Articulatory facet for the quadrate on the articular of (A) *H. xenostoma*, and (B) *H. serranus*.

with a moderately oblique jaw angle of 20°–30°. In *H. xenostoma* the articulatory surface of the articular is deeper and more nearly "U" shaped in lateral view; it lacks the posterior prolongation of its ventral border, but has a marked, near-conical eminence developed postero-medially. All these differences seem to be associated with the oblique angle of the jaw at rest, and the wide angle through which it can be abducted when the mouth is maximally protruded. The small eminence appears to function as a control for the degree of lateral movement of the dentary, particularly when that bone is dropped almost to the horizontal. The posterior vertical limb of the articular in *H. xenostoma* slopes forward at a much greater angle from the perpendicular, thus providing more space between this bone and the suspensorium.

On the basis of my material (two skeletons of *H. xenostoma*, and one each of *H. serranus* and *H. victorianus*) it appears that the horizontal length of the suspensorium (as measured in a horizontal plane from the mid-point of the hyomandibular to the articular surface of the quadrate) is greater in *H. xenostoma* than in the other two species. This could account, at least partly, for the greater prognacity of this species, whose lower jaw has the same relative length as that of *H. serranus* and *H. victorianus*. The angle of the hyomandibular relative to the perpendicular is similar in all three species.

The premaxilla has a slight median expansion of its dentigerous surface, and the pedicels are relatively shorter than those of *H. serranus*.

As compared with the dentary of *H. serranus* and *H. victorianus*, that of *H. xenostoma* is deeper and stouter, and the dentigerous surface has a more pronounced upward sweep towards the coronoid region.

The lower pharyngeal bone is triangular, and fairly stout; the dentigerous area is as long as broad or very slightly broader than long. Lower pharyngeal teeth are variable in form, usually with coarse, cylindrical necks and compressed, weakly cuspidate crowns; in some fishes, however, the crowns are distinctly cuspidate. Less commonly, the teeth are slender and compressed, with very weakly cuspidate crowns. The teeth are arranged in 22–24 rows.

Vertebral counts in 7 specimens are: 13 + 15 (f.1), 13 + 16 (f.5) and 13 + 17 (f.1), giving totals of 28–30.

Coloration: Live colours are known only for a single *juvenile female*; ground coloration silvery, shading to yellowish-grey dorsally, the dorsal surface of the snout dark grey. Dorsal fin dark hyaline, pelvics hyaline, anal yellow, caudal yellowish-grey. *Preserved coloration: Males* (*adult and sexually active*) have the ground coloration generally dusky over dark brown dorsally, and silver on the flanks and belly, the latter region together with the chest often with a dusky overlay; lower jaw and entire branchiostegal membrane also sooty. Snout and preoperculum sooty, but the upper lip is dark brown; operculum with a faint golden flush. A faint but dark and broad midlateral stripe runs along the flank from the posterior margin of the preoperculum to the caudal fin origin. Dorsal fin yellow-brown, with a sooty overlay on the spinous part, and black lappets; soft part with dark spots and dashes. Caudal dusky on its proximal threequarters, yellowish-brown distally. Anal light brownish-yellow, with a thin dark line along the base, and black lappets;

3 or 4 large, darkor whitesh ocelli are present, each with a narrow black outline. The ocelli are arranged in one or two rows. Pelvics entirely dusky.

Males (*adult but quiescent*) *:* have essentially the same coloration as active males, but some are lighter (that is, with more silvery flanks, and greyish branchiostegal membrane).

Females (*adult, and at various degrees of sexual activity*). Greyish-brown above, shading through silvery-grey on the flanks to gold below ; snout and preorbital region dark. On the flanks, a faint dark midlateral band (as in males) may be visible, and in addition, a fainter upper band running just above the upper lateral line. Dorsal fin yellowish-grey with a sooty overlay on the spinous part, and with black lappets ; soft dorsal sometimes darkly spotted. Caudal dark on the proximal two-thirds, lighter distally. Anal yellowish with a faint sooty overlay, sometimes with ill-defined dark spots in the position of the ocelli in males. Pelvics hyaline, usually with a dusky overlay.

Ecology. Habitat. The species is apparently confined to sheltered or relatively undisturbed water, being common in bays and gulfs where the water is less than 40 ft. deep, and the bottom is of soft mud, sand or shingle. Available records suggest that the species favours a mud substrate.

Food. Of the 21 fishes examined (from 9 localities), only 6 contained food in the guts. In each case the food comprised fragmentary fish remains, unidentifiable except in one instance (a small *Haplochromis* species).

Breeding. All fishes less than 160 mm. S.L. are immature ; one larger individual (a female 163 mm. S.L.) is also immature. Males and females appear to reach the same maximum adult size.

Affinities. The very oblique mouth, marked prognacity, and relatively deep body (at least in adults) serve to distinguish *H. xenostoma* from the majority of larger *Haplochromis* species in the lake. There is some resemblance between this species and *H. macrognathus* and *H. plagiostoma,* both species with an oblique mouth, and in the case of *H. macrognathus*, a prominent lower jaw.

Haplochromis xenostoma is readily distinguished from *H. macrognathus* by its broader head (interorbital width 20·4–27·5, M = 24·5% head *cf.* 16·5–22·2, M = 18·6% ; snout 1·2–1·5 times as long as broad, *cf.* 1·5–2·2 times in *H. macrognathus*), and its more oblique mouth. The neurocranium also differs, that of *H. macrognathus* being of the "*prognathus*" type, whilst the skull of *H. xenostoma* is clearly of the "*serranus*" type (see p. 111 and discussion on pp. 109–113 ; also Greenwood, 1962).

From *H. plagiostoma*, *H. xenostoma* differs in its larger adult size, longer and narrower snout (34·2–39·2, M = 37·4% head, *cf.* 28·2–35·5, M = 32·5%), more prominent and longer lower jaw (50·0–62·0, M = 57·0% head, *cf.* 44·0–54·5, M = 49·2% ; lower jaw rarely projecting in *H. plagiostoma*) and the greater number of teeth in the outer row of the upper jaw (56–94, M = 82, *cf.* 44–68, M = 57). Neurocranial form in these two species is similar (see p. 113).

Another species with an oblique mouth is *H. cavifrons.* It is distinguished from *H. xenostoma* by its unique mottled coloration, lack of prognacity, broader snout (as long as broad or slightly broader than long, *cf.* 1·2–1·5 times as long as broad), and fewer teeth (56–74, M = 63, *cf.* 56–94, M = 82). The profile of the head also differs (compare fig. 6 above with fig. 20 in Greenwood, 1962).

Phylogenetically, *H. xenostoma* could be derived from a species resembling *H. plagiostoma*; its affinities seem to lie more with the "*serranus*" group than with the "*prognathus*" group to which *H. macrognathus* belongs. (See also discussion on pp. 113).

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.257 (Paralectotype)	Entebbe	Degen
B.M. (N.H.) 1966.3.9.92–93	Napoleon Gulf, near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.88, 96–106	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.87	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.90–91	Off Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
	KENYA	
B.M. (N.H.) 1966.3.9.89	Naia Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.86	Nanga Bay (Kavirondo Gulf)	E.A.F.R.O.
B.M. (N.H.) 1966.9.9.85	Off mouth of Nzoia River	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.90 (Lectotype)	Locality unknown	Sir H. H. Johnston
B.M. (N.H.) 1966.3.9.94–95	Locality unknown	E.A.F.R.O.

Haplochromis pseudopellegrini sp. nov.

(Text-fig. 8)

HOLOTYPE: an adult male 139 mm. standard length, from Pilkington Bay (Uganda). B.M. (N.H.) no. 1966.2.21.2.

Named *pseudopellegrini* because of its resemblance to *H. pellegrini* Regan.

DESCRIPTION: based on 17 specimens (including the holotype) 98 to 150 mm. standard length.

Depth of body 29·0–33·5 (M = 30·9) per cent of standard length, length of head 32·4–37·0 (M = 33·8) per cent. Dorsal head profile gently curved (rarely straight) but interrupted by the prominent premaxillary pedicels.

Preorbital depth 19·1–22·4 (M = 20·4) per cent of head length, least interorbital width 20·4–27·1 (M = 23·9) per cent. Snout a little longer than broad (1·2–1·3 times), its length 35·1–39·0 (M = 37·1) per cent of head; eye diameter 18·5–25·4 (M = 20·6), depth of cheek 24·0–29·6 (M = 26·8) per cent.

Caudal peduncle 16·3–20·8 (M = 18·3) per cent of standard length, 1·3–2·0 (modal range 1·6–1·7) times as long as deep.

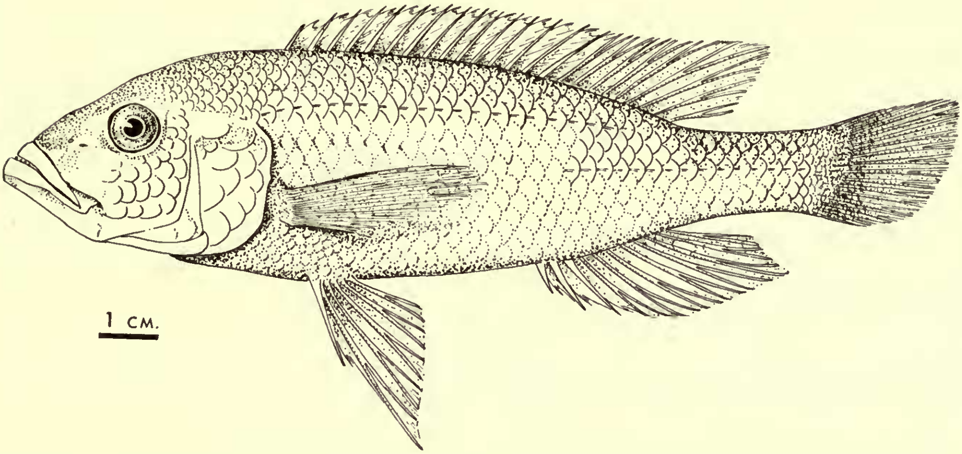

FIG. 8. *Haplochromis pseudopellegrini* ; this specimen shows extreme development of an obliquely truncate caudal fin. Drawn by Barbara Williams.

Mouth slightly oblique, lower jaw projecting a little. Premaxilla slightly expanded medially. Lower jaw 46·8–53·4 (M = 49·1) per cent of head, 2·0–2·6 (modal range 2·1–2·4) times as long as broad. Posterior tip of the maxilla reaching, or almost reaching the vertical through the anterior orbital margin, extending a little beyond this point in a few specimens.

Gill rakers : of variable form, from relatively slender to moderately stout (reduced to short knobs in one specimen), the upper four sometimes flat ; 9 (rarely 8 or 10) on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 32 (f.4), 33 (f.7), 34 (f.4) or 35 (f.1) scales. Cheek with 4 (less commonly 3, rarely 5) rows. Six or 7 (rarely 7½) scales between the dorsal fin origin and the upper lateral line, 7 (occasionally 6, rarely 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.1), 24 (f.4) or 25 (f.12) rays, comprising 15 (f.9) or 16 (f.8) spinous and 8 (f.1), 9 (f.12) or 10 (f.4) branched rays. Anal with 11 (f.10) or 12 (f.7) rays, comprising 3 spines and 8 (f.10) or 9 (f.7) branched elements. Pectoral 22·7–28·0 (M = 24·9) per cent of standard length. First branched ray of pelvic fin slightly produced in both sexes, proportionately more so in adult males. Caudal scaled over its proximal half ; in most specimens the fin is truncate or subtruncate but in a few the lower half, or the ventro-posterior corner, slopes obliquely forward and may also be rounded.

Teeth. The outer row of teeth in both jaws is composed of slender and slightly recurved unicuspids ; there are 35–52 (M = 44) teeth in the outer row of the upper jaw.

Inner teeth are also unicuspid, and are implanted at an angle varying from near vertical to almost horizontal, the latter condition being most common. There are 2 (rarely 3) rows of inner teeth in the upper jaw, and 1 or 2 rows in the lower.

Osteology. The neurocranium of *H. pseudopellegrini* shows some similarity with that of *H. mento* and other species in the "*prognathus*" group (see Greenwood, 1962, and p. 110), but at the same time it retains characteristics of the more generalized skull seen in *H. serranus* and its allies. In this respect it resembles the neurocranium of *H. prognathus*, but is slightly less "*mento*"-like. In general appearance and proportions it is similar to the neurocrania of *H. bayoni* and *H. dentex* but lacks the characteristically decurved ethmo-vomerine region of these species (see Greenwood, *op. cit.*).

The premaxilla is moderately beaked, that is, the dentigerous part of the bone is somewhat expanded medially; the pedicels are short, being about two-thirds the length of the dentigerous arm.

The lower pharyngeal bone is triangular, its dental surface is as long as broad or slightly longer than broad. Lower pharyngeal teeth are slender and compressed, those in the two median rows are slightly coarser than their lateral congeners; the teeth are arranged in 22–24 rows. Vertebral counts in 14 specimens are: 13 + 17 (f.4), 13 + 18 (f.1), 14 + 17 (f.9), giving totals of 30 and 31.

Coloration: Live colours are known only for *adult and sexually active males*, which have the dorsal surface of the head and body dark brown, the flanks and belly golden-yellow overlain by an orange-red flush on the chest and anterior flanks, and also on the operculum. Dorsal fin dark neutral with a slight orange flush. Caudal dark neutral, with a reddish flush at the base and over the ventral quarter of the fin. Anal neutral, with yellowish-red ocelli. Pelvics are sooty.

Preserved material: Males (*adult and active*): ground colour brownish overlying silver, silvery-yellow on the chest and belly, and on the operculum; rest of head (including the branchiostegal membrane) brownish with very faint traces of a lachrymal blotch. Dorsal fin hyaline, with a faint, narrow black band running from the tip of the eleventh spine to about the middle of the last branched ray (*i.e.* curving gently downwards). Caudal brownish to hyaline, dark on the proximal half. Anal hyaline, with faint traces of one or two whiteish-grey ocelli. Pelvics sooty, darkest on the anterior half.

Adult but quiescent males are light brown dorsally, shading to silvery below, some showing a faint but broad and dark midlateral stripe, and a fainter upper lateral band above the upper lateral line. The two lateral bands are connected by 4–6 vertical bars, which extend ventrally a little below the midlateral band; where the lines intersect, the lateral one is diffusely expanded. A faint lachrymal blotch is present below the anterior part of the orbit. All fins are yellowish-brown, the soft dorsal and the proximal part of the caudal are often darkly maculate. Anal with 2 or 3 faint, whiteish ocelli. Pelvics variable, from yellowish-brown to sooty.

Ecology. Habitat. The species is recorded from four localities only. Two of these are shallow, sheltered bays, one is a fairly exposed, offshore and deep (90 ft.) channel, and the fourth is not fully documented except for a note that the nets were set in water about 20 ft. deep. In all, the substrate is of organic mud.

Food. Fourteen specimens were examined, and of these only two contained food, very fragmentary and generically unidentifiable fish remains.

Breeding. Little information is available on the reproductive biology of this species. The sex of the smallest specimen (98 mm. S.L.) is indeterminable; the others (132–153 mm.) are all adults, and only two are females. The two largest fishes are males.

Affinities. In general appearance *H. pseudopellegrini* closely resembles *H. pellegrini*; however, it reaches a much larger adult size, and the preserved coloration of adult males is much lighter (uniformly dark brown, nearly black in *H. pellegrini*, light brown over silver in *H. pseudopellegrini*). The species also differ in certain morphometric characters. *Haplochromis pseudopellegrini* has a longer snout (35·1–39·0, M = 37·1% head, *cf.* 30·8–36·0, M = 34·0%), a longer and more slender caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 13·2–17·8, M = 15·4%; length/depth ratio 1·3–2·0 [modal range 1·6–1·7], *cf.* 1·1–1·5 [mode 1·3]); unfortunately it is not possible to determine whether, at least in part, these differences are attributable to the larger size of the *H. pseudopellegrini* specimens. There are fairly marked interspecific differences in neurocranial form, and these do not appear to be influenced by size. The neurocranium in *H. pellegrini* shows much greater departure from the generalized condition than does that of *H. pseudopellegrini* (for *H. pellegrini*, see Greenwood, 1962).

In its general facies, *H. pseudopellegrini* resembles *H. guiarti*, *H. altigenis*, *H. dentex*, *H. mento* and *H. gowersi*, particularly the former species.

The differences separating *H. pseudopellegrini* from *H. altigenis* are discussed on p. 64; *H. pseudopellegrini* could represent the ancestral morphotype from which *H. altigenis* evolved.

From *H. guiarti* it is distinguished by its different neurocranial form, and the following: slightly longer snout (35·1–39·0, M = 37·1% head, *cf.* 31·7–37·5, M = 34·4%), slightly narrower interorbital region (20·4–27·1, M = 23·9% head, *cf.* 23·4–30·2, M = 27·4%), longer and narrower lower jaw (48·6–53·4, M = 49·1% head, *cf.* 39·2–48·2, M = 44·4%; length/breadth ratios 2·0–2·6 [modal range 2·1–2·4] *cf.* 1·5–2·3 [mode 2·0]), fewer teeth in the outer row of the upper jaw (35–52, M = 44, *cf.* 48–74, M = 62).

From *H. gowersi* it differs in head shape (and neurocranial form), and in having a much shorter head (34·2–37·0, M = 33·8% standard length, *cf.* 35·8–38·4, M = 37·0%), a broader snout, a larger eye (18·5–23·4, M = 20·6% head, *cf.* 15·5–19·3, M = 17·5%), a slightly shallower cheek (24·0–29·6, M = 26·8% head, *cf.* 27·8–33·3, M = 29·5%), and a longer caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 13·3–17·6, M = 14·8%).

From *H. dentex*, *H. pseudopellegrini* differs, superficially, by its less strongly decurved dorsal head profile. At a deeper level, there are differences in the shape of the neurocranium, that of *H. dentex* having a sharply decurved ethmoid-vomer region (see Greenwood [1962], p. 168 and fig. 25); but in other respects, the neurocrania of the two species are similar. Other interspecific differences lie in the more numerous and closely set teeth of *H. pseudopellegrini* (35–52, M = 44, *cf.* 32–48, M = 36), its deeper body (29·0–33·5, M = 30·9% of standard length, *cf.* 24·6–29·5, M = 26·7), and the greater posterior extension of the maxilla in this species (posterior maxillary tip reaching anterior orbital margin or to below the eye, *cf.* not reaching the orbital margin).

From *H. estor*, *H. pseudopellegrini* differs, principally, in having a shorter head

(32·4–37·0, M = 33·8% standard length, *cf.* 37·2–38·5, M = 37·8%), a shorter lower jaw (46·8–53·4, M = 49·1% head, *cf.* 54·2–57·5, M = 55·5%), and a longer caudal peduncle (16·3–20·8, M = 18·3% standard length, *cf.* 14·3–16·1, M = 15·8%). Neurocranial form in the two species differs, that of *H. estor* belonging to the "*prognathus*" group, whilst that of *H. pseudopellegrini* has stronger affinities with the "*altigenis*"-type (see p. 110).

The resemblance between *H. pseudopellegrini* and *H. mento* is probably the most distant of all. Osteologically, there is a clear-cut difference in neurocranial form (like that distinguishing *H. pseudopellegrini* and *H. estor*), and in most specimens the external head shape is distinctive (*cf.* fig. 12 in Greenwood [1962] with Text-fig. 8 above). Nevertheless, most cephalic morphometric characters are similar in the two species, although the snout of *H. pseudopellegrini* is broader (length/breadth ratio 1·1–1·3 *cf.* 1·5–1·8 in *H. mento*). The outer teeth in *H. mento* are stouter and more strongly curved than those of *H. pseudopellegrini*; the range for the number of outer upper jaw teeth overlaps in the two species, but the mean for *H. pseudopellegrini* is lower (44 *cf.* 52).

Phyletically, *H. pseudopellegrini* appears to be a derivative from an *H. guiarti*-like stem, and thus shows relationship with *H. bayoni* and *H. dentex*. However, unlike these species it also shows relationship with both *H. altigenis* and *H. pellegrini*. Structurally, *H. pseudopellegrini* could represent an ancestral level in the evolution of *H. altigenis*.

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.299–310	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.296	Trawl in Buvuma Channel off Nasu Point	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.297	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.2 (Holotype)	Pilkington Bay . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.298	Sesse Islands	E.A.F.R.O.

Haplochromis altigenis Regan, 1922

(Text-figs. 9 and 10)

Paratilapia longirostris (part): Boulenger, *Cat. Afr. Fish.*, **3**, 332.
Pelmatochromis spekii (part): Boulenger, 1915, *op. cit.*, *tom. cit.*, 417.
Haplochromis altigenis Regan, 1922, *Proc. zool. Soc. Londn.*, 175, Pl. 1.

LECTOTYPE: a male, 186 mm. standard length from Bunjako (Uganda), collected by Degen. B.M. (N.H.) reg. no. 1906.5.30.294.

DESCRIPTION: based on 25 specimens (including the lectotype and paralectotype), 100–202 mm. standard length.

Depth of body 28·4–34·7 (M = 31·5) per cent of standard length, length of head 36·7–39·5 (M = 38·2) per cent. Dorsal head profile gently curved, rather variable in its shape, tending to slope more steeply in large fishes which therefore have more rounded profiles; the two type specimens have the most strongly sloping head

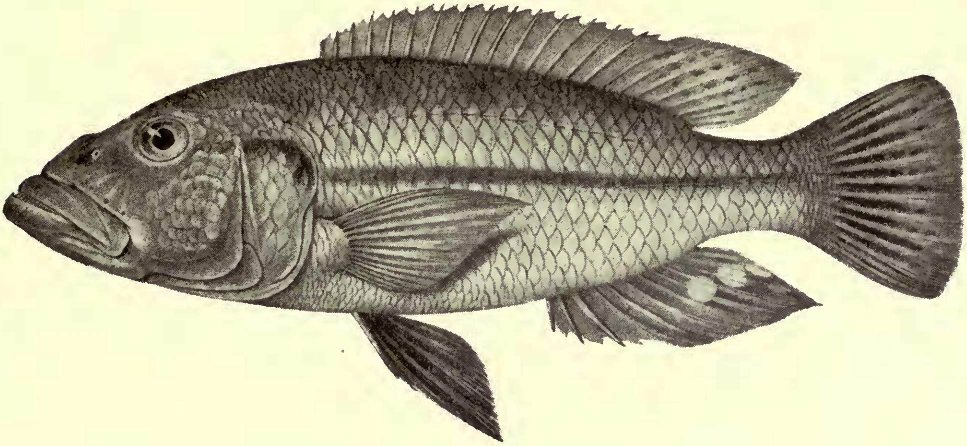

FIG. 9. *Haplochromis altigenis* ; lectotype, about ·57 times natural size. From Regan, *Proc. zool. Soc.*

profiles (*ca* 40°) ; most other specimens lie in the range 30°–35°. The premaxillary pedicels are prominent, and clearly break the outline of the profile. Altogether, one is left with the impression of a heavy-headed fish.

Preorbital depth 17·6–23·7 (M = 19·9) per cent of head length, least interorbital width 17·4–25·0 (M = 20·2) per cent. Snout 1·1–1·3 times as long as broad, its length 36·6–42·2 (M = 39·3) per cent of head, eye diameter 16·9–21·7 (M = 19·2), depth of cheek 25·6–34·5 (M = 30·5) per cent. Cheek depth may show positive allometry with standard length in fishes > 180 mm. ; the three largest fishes have the deepest cheeks.

Caudal peduncle 12·4–16·0 (M = 14·7) per cent of standard length, 1·2–1·4 (mode 1·3) times as long as deep.

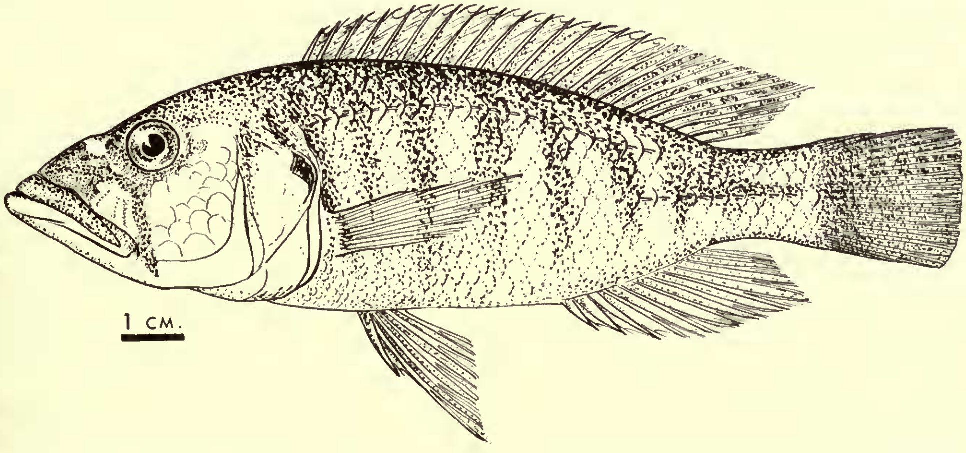

FIG. 10. *Haplochromis altigenis*, to show the usual head profile in fishes less than *ca.* 180 mm. S.L. Drawn by Barbara Williams.

Mouth slope variable, from near horizontal to moderately oblique (20°–30°). Lips slightly thickened, the premaxilla expanded medially. Lower jaw generally projecting (but jaws equal anteriorly in some specimens), its length 51·0–55·8 (M = 52·7) per cent of head, 1·8–2·4 (modal range 1·9–2·0) times as long as broad. Posterior tip of the maxilla almost reaching the vertical through the anterior orbital margin (reaching this point in a few specimens).

Gill rakers : stout (finer in the two smallest fishes), the upper 1–4 sometimes flattened and anvil-shaped ; 8 or 9 (rarely 7 or 10) on the lower part of the first arch.

Scales : ctenoid ; lateral line with 31 (f.7), 32 (f.13) or 33 (f.4), cheek with 4–6 (mode 5) rows. Six to 8 scales between the upper lateral line and the dorsal fin origin ; chest and anterior belly scales small, 7 or 8 (rarely 9) between the pectoral and pelvic fin bases.

Fins : Dorsal with 24 (f.8), 25 (f.16) or 26 (f.1) rays, comprising 15 (f.22) or 16 (f.3) spinous and 9 (f.10) or 10 (f.15) branched rays. Anal with 11 (f.2), 12 (f.22) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.22) or 10 (f.1) branched elements. Pectoral 20·1–26·2 (M = 22·6) per cent of standard length. Pelvics with the first branched ray produced, usually more so in males but almost as elongate in some females. Caudal subtruncate, scaled on its proximal half.

Teeth. In the size range of fishes studied, all teeth in the outer row of both jaws are stout, unicuspid and curved. There are 40–60 (M = 50) teeth in the outer row of the upper jaw.

The inner teeth of the two smallest fishes (90 and 119 mm. S.L.) are predominantly unicuspids, but some weakly tricuspid teeth occur in both jaws. In all other specimens, only unicuspids are found ; these are moderately large, curved and implanted obliquely. The inner tooth rows are often irregularly arranged, with 3 (rarely 4) rows in the upper jaw, and 2 or 3 in the lower.

Osteology. The neurocranium of *H. altigenis* resembles that of *H. bayoni*, but is relatively broader in the otic region. Thus, although it shows some of the characters associated with the *H. mento*-type skull (see Greenwood, [1962], fig. 25) it still retains the curved preorbital profile, greater preorbital skull depth, and broad otic region of the more generalized neurocranium. In these characters it also resembles the neurocranium of *H. pseudopellegrini*.

The dentary and premaxillary show no outstanding characters. The former is a stout bone, and the dentigerous surface of the latter is but moderately expanded medially (less so, for example, than in *H. bayoni*).

The dentigerous surface of the lower pharyngeal bone is as broad as long but is broader than long in large fishes. Anteriorly this surface narrows rather abruptly so that the apex of the dentigerous triangle is produced into a narrow " stem ". The lower pharyngeal teeth are rather coarse, somewhat compressed and clearly but weakly cuspidate.

Vertebral counts in 7 specimens are : 13 + 16 (f.5) and 13 + 17 (f.2), giving totals of 29 and 30.

Coloration. Live colours are unknown. *Preserved material : Males (adult and sexually active):* ground coloration a very dark brown, almost black on the dorsal surface and snout, and with a sooty overlay on the chest. Lower jaw and branchiostegal membrane pinkish-brown ; margin of the preoperculum outlined in dark brown. Dorsal fin yellow-brown, lappets black, and with a faint black outline to the margin of the soft part. Caudal darker yellow-brown (darkest proximally). Anal yellow-brown, with 2 large, dead-white ocelli. Pelvics very dark brown, appearing black when folded. Pectorals dark brown (dark pectorals are unusual).

Males (*adult but sexually quiescent*) have a light brown ground coloration, darker on the dorsal surface of the snout, head and body. A prominent, but narrow, dark lachrymal stripe runs from the lower anterior border of the eye, passes almost vertically downwards behind the posterior tip of the maxilla to end on the dentary ; a slightly broader dark bar lies immediately anterior to the vertical limb of the preoperculum. The lower jaw and branchiostegal membrane are very light brown ; the chest is somewhat dusky. The flanks and caudal peduncle are crossed by seven very faint, moderately broad dark bars ; these extend (on the flanks) from the dorsal fin base almost to the ventral body outline. Dorsal fin yellow-brown, the lappets black and the soft part darkly maculate. Caudal yellowish-brown, darkest on the proximal half. Anal dark yellow-brown. Pelvics dark brown, nearly black, on the anterior half, otherwise light yellow-brown.

Male (*immature*) *:* essentially as for females (see below), but with black lappets on the dorsal fin, the caudal uniformly light but with some dark spots on the upper fifth, 3 faint whiteish ocelli on the anal, and a dusky overlay on the pelvics.

Note on the coloration of the type specimens. Both these specimens are males, but both are now a pale silver, shading to white. One specimen (that illustrated by Regan, see fig. 9 above) has a very faint midlateral stripe, which is now much fainter than is shown in the figure. Both fishes have dusky pelvics. In one, there are five, large, dead-white ocelli (arranged in three rows) on the anal fin, and in the other there are four (in two rows). The difference in coloration between these specimens and those described above is, presumably, due both to time and to the fact that the types were not fixed in formol but in alcohol.

Females (*immature and adult*) *:* ground coloration light brown, darkest dorsally, and shading to yellowish-silver on the chest and belly. Lachrymal and preopercular stripes are as described for males, but in addition there are two, faint, parallel dark bands across the snout. The lower jaw and branchiostegal membrane are light yellow-brown. A faint dark midlateral band runs along the flank from slightly behind the opercular margin to the base of the caudal fin (sometimes extending onto the fin itself), and is crossed by 8 to 10, moderately broad vertical bars which extend from the dorsal fin base to about the level of the pectoral fin. Dorsal fin light greenish-brown, the soft part darkly maculate. Caudal yellow-brown on its distal quarter to third, dark brown basally. Anal greenish-brown. Pelvics light yellow-brown, somewhat darker along the anterior margin.

Three fishes (140, 148 and 149 mm. S.L.) caught on two occasions off Kisigala; Point, North Kome Island, show typical piebald coloration of black on silver ; all three are immature females. These are the first known examples of piebald polychromatism amongst the piscivorous species-groups of Lake Victoria *Haplochromis*, although the phenomenon is recorded from other trophic and phyletic lines (see Greenwood, 1956, 1957, 1959, and p. 95 below).

Ecology. Habitat. The species occurs over both hard and soft substrates in sheltered bays and gulfs, as well as off-shore in places where the water is relatively undisturbed ; apparently it does not occur at depths of over 50 ft.

Food. Eleven of the 26 specimens examined (from 15 localities) contained food in the gut. In all cases this consisted of finely macerated fish remains, identifiable as cichlids in three specimens, and as *Haplochromis* species in six others.

Breeding. Haplochromis altigenis is a female mouth breeder. Fishes less than 145 mm. S.L. are immature, or, in the upper levels of the range, show early signs of maturation. The largest specimen (202 mm. S.L.) is a female, but both sexes occur in the size range 170–194 mm.

Affinities. At least superficially, four species, *H. pseudopellegrini*, *H. estor*, *H. dichrourus* and *H. gowersi*, closely resemble *H. altigenis*. A fifth species, *H. squamulatus* shows a more distant resemblance.

Similarities between *H. altigenis* and *H. dichrourus* are considered elsewhere (see p. 68) ; the resemblances between these species may indicate a fairly close phyletic relationship.

From *H. pseudopellegrini*, *H. altigenis* is distinguished by its longer head (36·7–39·5, M = 37·2% of standard length, *cf.* 32·4–37·0, M = 33·8%), deeper cheek (25·6–34·5, M = 30·5% head, *cf.* 24·0–29·0, M = 26·8%), longer lower jaw (51·0–55·8, M = 52·7% head, *cf.* 46·8–53·4, M = 49·1%) and its shorter and deeper caudal peduncle (12·4–16·0, M = 14·7% standard length, *cf.* 16·3–20·8, M = 18·3%, length/depth ratio 1·2–1·4 [mode 1·3] *cf.* 1·3–2·0 [modal range 1·6–1·7]). The neurocranium in the two species is generally similar. It seems that *H. altigenis* could have evolved from an *H. pseudopellegrini*-like ancestor.

From *H. estor*, *H. altigenis* differs in its longer snout (36·6–42·2, M = 39·3% head, *cf.* 34·5–37·0, M = 36·2%), smaller eye (16·9–21·7, M = 19·2% head, *cf.* 22·8–25·4, M = 24·5%), much deeper cheek (25·6–34·5, M = 30·5% head, *cf.* 22·8–25·4, M = 24·5%) and slightly shorter lower jaw (51·0–55·8, M = 52·7% head, *cf.* 54·2–57·5, M = 55·5%). There are fairly marked differences between the neurocrania of the two species, that of *H. estor* being of the " *prognathus* " type.

Superficially, the resemblances between *H. gowersi* and *H. altigenis* are great, and some difficulty may be experienced in separating certain specimens of the two species. However, there are distinct differences between modal specimens of the two species, and there is a clear difference in neurocranial form ; the skull of *H. gowersi* is of the " *prognathus* " type. This difference in neurocranial shape probably accounts for the more declivous snout and dorsal head profile of *H. altigenis*, and the greater prominence of the premaxillary pedicels in this species. In addition to these qualitative differences, *H. altigenis* differs from *H. gowersi* in having the interorbital width equal to or slightly greater than the preorbital depth (interorbital less than preorbital in *H. gowersi*), a broader head (greatest width, measured at about the middle of the operculum, 41·5–45·5, M = 42·7% head, *cf.* 35·6–39·0, M = 36·8) ; the greater head breadth is also reflected in the broader lower jaw of *H. altigenis*.

Haplochromis squamulatus and *H. altigenis* both have noticeably rounded head profiles, and very small chest and anterior belly scales. However, they differ in several morphometric characters. *Haplochromis altigenis* has a longer head, narrower interorbital, longer snout, deeper cheek and a longer lower jaw (see p. 87). The neurocrania show several interspecific differences (that of *H. squamulatus* showing affinities with the neurocrania of *H. martini* and *H. michaeli*) and there are marked differences in preserved coloration.

Considering the evidence available, both morphometric and osteological, it seems *H. altigenis* could have evolved from an *H. pseudopellegrini*-like stem ; certainly its neurocranial form does not favour a closer association with *H. estor* and *H. gowersi* than with *H. pseudopellegrini*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.294 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1906.5.30.295 (Paralectotype)	Bunjako	Degen
B.M. (N.H.) 1966.3.9.220–227	Napoleon Gulf, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.228–235	Karenia Beach, near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.215–216	Near Ramafuta Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.219	Pilkington Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.218	Manadu Island	E.A.F.R.O.
B.M. (N.H) 1966.3.9.213–214	Off Entebbe harbour . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.217	Mwanza Harbour . . .	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.211–212	Locality unknown . . .	E.A.F.R.O.

Haplochromis dichrourus Regan, 1922

(Text-fig. 11)

Paratilapia serranus (part) : Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 334.
Haplochromis dichrourus Regan, 1922, *Proc. zool. Soc. Londn.*, 178, fig. 6.

HOLOTYPE : a juvenile female, 113·0 mm. S.L., from Buganga ; B.M. (N.H.) reg. no. 1906.5.30.265.

DESCRIPTION : based on eight specimens (including the holotype), 84–186 mm. S.L.

Depth of body 28·6–35·5 (M = 32·1) per cent of standard length, length of head 35·2–37·7 (M = 36·6) per cent. Dorsal head profile convex, sloping steeply (*ca* 40°) especially in the snout region ; premaxillary pedicels prominent and breaking the outline of the profile.

Preorbital depth 16·4–21·0 (M = 18·7) per cent of head, least interorbital width 18·0–24·6 (M = 21·3) per cent. Snout 1·10–1·25 times as long as broad, its length

34·1–41·0 (M = 37·4) per cent of head, eye diameter 19·4–24·6 (M = 21·1), depth of cheek 23·0–30·6 (M = 27·6) per cent.

Caudal peduncle 12·4–17·2 (M = 15·2) per cent of standard length, 1·1–1·5 times as long as deep.

Mouth slightly oblique (20°–30°), lips thickened, premaxilla slightly expanded medially. Lower jaw projecting, its length 49·0–54·0 (M = 52·7) per cent of head, 1·8–2·6 (no distinct mode) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior margin of the orbit, or to below the anterior part of the eye.

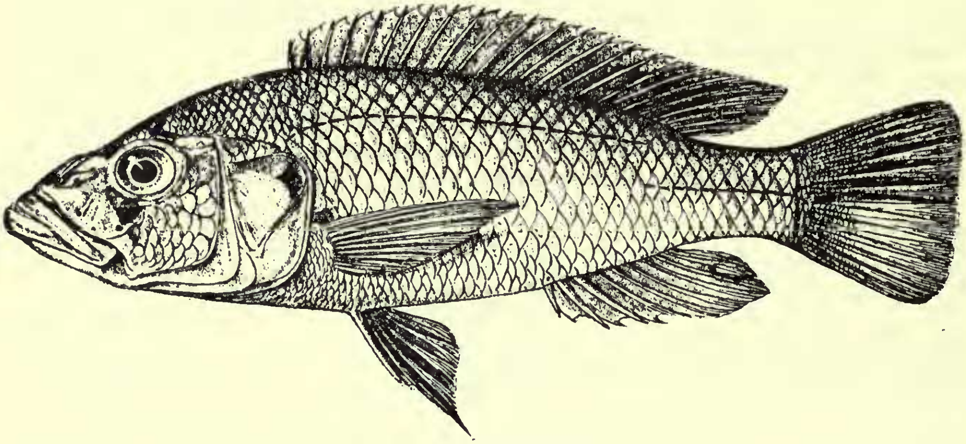

FIG. 11. *Haplochromis dichrourus*; holotype, about ·93 times natural size. From Regan, *Proc. zool. Soc.*

Gill rakers: stout, the lower 2 or 3 reduced, the upper 3 or 4 flat and expanded in some specimens; 8 or 9 (mode) on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 32 (f.2), 33 (f.4) or 34 (f.2), cheek with 3 (f.1), 4 (f.1), 5 (f.5), or 6 (f.1) rows. Seven to 9 scales between the upper lateral line and the dorsal fin origin, 6–9 (mode 8) between the pectoral and pelvic fin bases; scales on the chest and belly small.

Fins: Dorsal with 25 rays, comprising 15 (f.1) or 16 (f.7) spinous and 9 (f.7) or 10 (f.1) branched rays. Anal with 11 (f.2), 12 (f.5) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.5) or 10 (f.1) branched elements. Pectoral fin 21·2–27·3 (M = 23·7) per cent of standard length. Pelvics with the first, and to a lesser degree, the second branched rays produced, slightly so in females and markedly elongate in males. Caudal truncate or subtruncate.

Teeth. In all specimens the outer teeth (numbering 48–70, M = 58 in the upper jaw) are unicuspid, slender and very strongly curved (the tips of the anterolateral premaxillary teeth are not visible when the specimen is viewed laterally).

The inner teeth in fishes > 149 mm. S.L. are all unicuspid, curved and obliquely implanted. In the four smaller specimens, the 113 mm. fish (holotype) has mostly tricuspids in the upper jaw and an admixture of tri- and unicuspids (the latter predominating) in the lower jaw ; the 84, 101 and 121 mm. specimens have a mixture of unicuspids and weakly bicuspids in both jaws ; as in the larger fishes, these teeth are curved and obliquely implanted. The inner teeth are arranged in 1–3 series in the upper jaw, and in 2 or 3 in the lower (in a single row in one fish).

Osteology. With so few specimens available, it has not been possible to prepare a complete skeleton, but radiographs have been studied.

The lower pharyngeal bone is fine, with a triangular dentigerous surface which is equilateral or slightly broader than long. The lower pharyngeal teeth are slender, with cylindrical necks and slightly compressed weakly cuspidate crowns, and are arranged in 20–22 rows. Vertebral counts in 5 specimens are : 13 + 16 (f.1) and 13 + 17 (f. 4), giving totals of 29 and 30.

Ecology. Habitat. The species has a wide depth range, from 10–90 feet. It is found in both sheltered and exposed places (including beaches) over sand and shingle substrata.

Food. Of the five specimens examined (from four localities) four contained food in the gut. In three fishes this consisted solely of fish remains (*Haplochromis* sp.), and in the fourth fish-remains (a cichlid) and fragments of larval insects (one probably a dragon-fly, the other Ephemeroptera).

Breeding. Little information is available ; three of the smallest fishes (101, 113 and 121 mm. S.L.) are immature females.

An unusual feature of this species is the coloration of females, which, at least in preserved specimens, seems to be as polychromatic as that of males, and certainly more complex than the female coloration of other species (except, perhaps, *H. chromogynos*).

Coloration. The only information on live colours is provided by brief field notes made on a sexually active male caught in deep water near Soswa island. In this fish the median fins and back were described (by Mr. J. D. Kelsall) as vivid flame red, the belly as jet black.

Preserved Colours : Males. The most extreme pattern is shown by a fish which, although adult, is in an early stage of sexual activity. The upper part of the head (above the level of the lower orbital rim) brownish, snout yellowish and crossed by a thin, well-defined and dusky bar ; running parallel with the premaxillary pedicels are a pair of short, dark bars, each of which (at about the level of the pedicel tips) broadens somewhat and curves sharply at right angles to meet the orbit. The lower part of the head (cheeks, preorbital and the entire operculum) jet black. This colour extends onto the chest but does not reach above the level of the pectoral fin base. Immediately behind the pectoral fin, the margin of this black area curves ventrally but rises again above the vent so that the posterior half of the body is black on its lower half. On the caudal peduncle the dark area rises again to cover about the entire lateral aspect. Above the black areas the body is brownish. Dorsal and caudal fins are dark yellow-orange, with a narrow black crescent at the caudal base. The anal fin is a similar colour, with two ocelli, each outlined by a narrow black margin. Pelvics jet black, except for the yellowish innermost ray of each side.

In two other males (both sexually active, with convoluted testes and therefore thought to be more mature than the specimen above) the head and anterior half of the body are light orange-brown the posterior half and the caudal peduncle dusky brown. A well-defined black band crosses the snout (just above the upper lip) to the anterior margin of the preorbital bone. Another transverse black band at the level of the pedicel tips, runs from orbit to orbit. An interrupted band extends from the upper posterior margin of the orbit across the nape. A dusky, nearly vertical lachrymal stripe is present. The branchiostegal membrane and chest are black, but the belly is brown. Dorsal fin yellowish, the soft part is maculate, the spots being clear. Anal yellowish but dusky along its base, and with two, hyaline ocelli (set, in one specimen, in the dark basal zone). Caudal yellowish-grey, but with a broad, dusky band at its base. The pelvics are black except for the distal half of the membrane between the last two rays.

Females (*adult and immature*) *:* body and head dark grey-brown with a blueish hue. Branchiostegal membrane and chest dusky as are the lower parts of the operculum, preoperculum and interoperculum. Faint traces of snout and lachrymal bands (like those of males) are visible, as is a nuchal bar. Dorsal fin greyish to light sooty, the lappets dark. Anal pale orange with a single, well-defined, dead-white ocellus. Caudal with a dark base, the upper half grey and the lower orange. Pelvics light sooty, the pigment most concentrated on the anterior half of the fin.

Affinities. The anomalous coloration of female *H. dichrourus* was commented upon above. Apart from the relatively infrequent piebald females in certain species, and the occurrence of a piebald coloration as the usual one in females of *H. chromogynos* (see Greenwood, 1959), I know of no other species in Lake Victoria with colourful females.

In its gross morphology, *H. dichrourus* closely resembles *H. altigenis* although there are marked differences in the preserved coloration of the females. Both species have very small chest scales. They differ in that the maxilla of *H. dichrourus* reaches further posteriorly (rarely reaching the orbit in *H. altigenis*) and the premaxilla is not markedly expanded medially. Also, the teeth in *H. dichrourus* are more strongly curved, so that when viewed laterally, their tips are hidden ; in *H. altigenis*, the tips can always be seen.

The two smallest fishes resemble specimens of *H. pellegrini* of a similar size. They are, however, distinguished by their more slender and much more strongly recurved outer jaw teeth (in *H. pellegrini* these teeth have a gentle curvature confined to the distal part), and by having the maxilla extending further posteriorly (to below the anterior orbital margin). Also, in *H. dichrourus* the premaxillary pedicels are more prominent, and there are differences in preserved coloration.

Phyletically, *H. dichrourus* could be related to *H. altigenis* and *H. pellegrini*.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.265 (type)	Buganga	Degen
B.M. (N.H.) 1966.3.9.186	Jinja, off golf course . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.187	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.188–9	Karenia, Napoleon Gulf . .	E.A.F.R.O.

Tanzania

B.M. (N.H.) 1966.3.9.185	Off Soswa Island . . .	J. D. Kelsall
B.M. (N.H.) 1966.3.9.183–4	Beach N. of Majita . . .	E.A.F.R.O.

Haplochromis paraguiarti sp. nov.

(Text-fig. 12)

Holotype : an adult male 130 mm. standard length, from a beach near Nasu Point, Buvuma Channel (Uganda); B.M. (N.H.) reg. no. 1966.2.21.6.

Named *paraguiarti* because of its close superficial resemblance to *H. guiarti*.

Description : Based on 31 specimens (including the holotype), 70–156 mm. standard length.

Depth of body 31·7–36·6 (M = 34·1) per cent of standard length, length of head 33·0–36·8 (M = 34·8) per cent. Dorsal head profile straight or very slightly curved, the premaxillary pedicels forming a slight prominence.

Preorbital depth 14·5–19·5 (M = 16·9) per cent of head length, least interorbital width 22·9–27·7 (M = 25·3) per cent. Snout as long as broad or slightly longer (1·2 times), its length 31·0–36·2 (M = 33·5) per cent of head, eye diameter 23·8–28·6 (M = 26·2), depth of cheek 20·0–26·1 (M = 23·8) per cent.

Caudal peduncle 14·7–18·6 (M = 16·6) per cent of standard length, 1·3–1·9 (modal range 1·3–1·5) times as long as deep.

Mouth horizontal or slightly oblique, the jaws equal anteriorly. Lower jaw 41·0–48·6 (M = 45·0) per cent of head, 1·7–2·4 (modal range 1·9–2·1) times as long as broad. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin, occasionally extending to below the eye. Premaxilla slightly expanded medially.

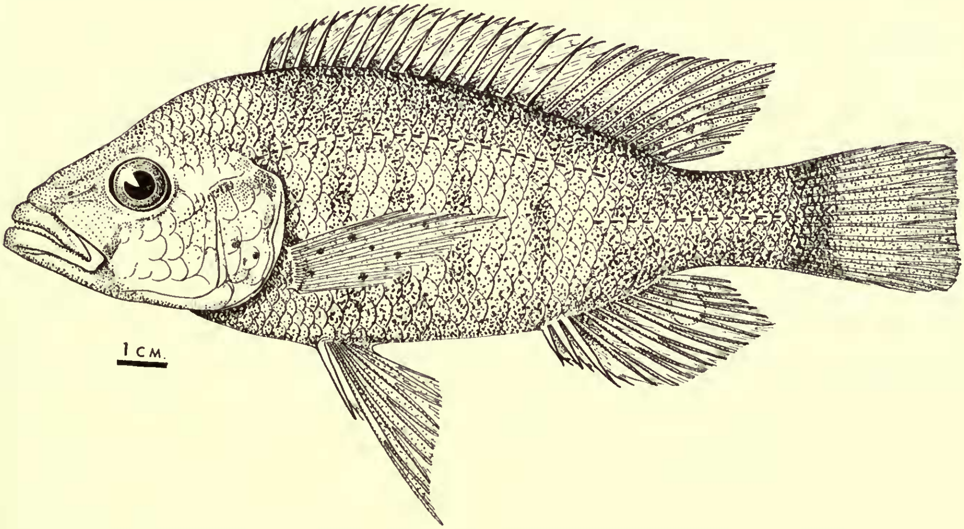

Fig. 12. *Haplochromis paraguiarti*. Drawn by Barbara Williams.

Gill rakers : moderately stout (relatively slender in fishes less than 90 mm. S.L.), the upper 4–6 flat and sometimes branched in fishes over 115 mm. S.L., the lower 1 or 2 reduced ; 8–10 (mode 9), rarely 11, on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 (f.4), 32 (f.12), 33 (f.12) or 34 (f.3) scales, cheek with 3 or 4 (rarely 2 or 5) rows. Five or 6 (rarely 6½) scales between the upper lateral line and the dorsal fin origin, 6 or 7 between the pectoral and pelvic fin bases. (Because many specimens were damaged during capture by gill-nets, the last two counts are based on only 17 specimens).

Fins : Dorsal with 23 (f.1), 24 (f.8), 25 (f.19) or 26 (f.3) rays, comprising 15 (f.21) or 16 (f.10) spinous and 8 (f.1), 9 (f.15) or 10 (f.15) branched rays. Anal with 11 (f.6), 12 (f.23) or 13 (f.2) rays, comprising 3 spines and 8 (f.6), 9 (f.23) or 10 (f.2) branched elements. Pelvic fins with the first unbranched ray slightly produced in the adults of both sexes, but proportionately more so in males. Pectoral 24·3–30·0 (M=26·3) per cent of standard length. Caudal truncate or subtruncate, scaled on its basal half to two-thirds.

Teeth : The form of the teeth in the outer row of both jaws shows some correlation with standard length. Only bicuspids (with a few tricuspids posterolaterally in the upper jaw) are found in fishes 70–75 mm. S.L. Unicuspids anteriorly, with bicuspids laterally are characteristic of most fishes 84–113 mm. S.L. (and in one exceptional individual 144 mm. S.L.). In most specimens over 112 mm. S.L., only unicuspids occur, but this is also the condition in a few fishes between 99 and 112 mm. S.L. The unicuspids are moderately stout teeth, and are only slightly curved. There are 42–62 (M = 54) outer teeth in the upper jaw.

Teeth in the inner rows are relatively large ; tricuspids predominate in fishes of all sizes, but in specimens over 120 mm. S.L. weakly tricuspids are commoner than the distinctly tricuspid ones, and some unicuspid teeth also occur (especially in the outermost row of the inner series). There are 3 or 4 inner rows in the upper jaw, and 2 or 3 (less frequently 1 row) in the lower.

Osteology : The neurocranium of *H. paraguiarti* is identical with that of *H. acidens* (see p. 75). It differs somewhat from the presumed generalized piscivore skull of *H. guiarti*, and shows some of the characters found in the more specialized type of *H. prognathus*. It is, in fact, almost intermediate between the two types.

The premaxilla has a less pronounced medial expansion than in *H. acidens*, but as in that species it has long pedicels (as long as the horizontal dentigerous arms) which meet the horizontal arms at an appreciable angle. In these characters the premaxilla of *H. acidens* differs from that bone in the generalized species like *H. guiarti* and *H. serranus*.

The lower pharyngeal bone is slender, its dentigerous surface slightly broader than long. The teeth are fine, slender, compressed and clearly bicuspid, only those in the posterior one or two rows of the median series are enlarged. There are 26–30 (mode 28) rows of lower pharyneal teeth.

Vertebral counts for 6 specimens are : 13 + 17 (f.4) and 14 + 16 (f.2), giving a total of 30.

Coloration : live colours unknown. *Preserved material : Males (adult and sexually active) :* ground colour dark sooty, almost uniformly so except for a lighter (dusky gold) patch on the midflank, crossed by four, faint and narrow vertical stripes. Branchiostegal membrane dark (darker below the opercular series than between the jaws). A very faint, near vertical lachrymal stripe runs from the anterior orbital margin to behind the posterior tip of the maxilla. Dorsal fin dusky, lappets black, the soft dorsal maculate. Caudal dark. Anal dusky, but lighter than the dorsal except for a narrow band along the base, and over the spinous part ; two or three greyish ocelli present. Pelvics dusky, the proximal threequarters almost black, the distal quarter lighter.

Males (adult but quiescent) : ground colour dusky silver-grey, darkest dorsally ; cheek bright silver. A faint lachrymal stripe present. Dorsal fin greyish-dusky, darkly maculate between the last four spines and all the branched rays. Caudal dark. Anal dark hyaline, with two or three greyish ocelli. Pelvics sooty, darkest on the leading edge.

Females (adult) : ground colour silver grey, darker dorsally : cheek bright silver (*i.e.* like quiet males but lighter and brighter). Dorsal fin dark hyaline, with dark spots on the soft part. Caudal dark hyaline, weakly to distinctly maculate. Anal and pelvic fins hyaline.

Females (juvenile) : Two small (75 mm. S.L.) specimens have colours like those of adult females, but with traces of 7 or 8 vertical bars on the flanks and caudal peduncle ; these bars reach the dorsal outline but do not extend ventrally below the level of the pectoral fin base.

Ecology. Habitat. Most records of *H. paraguiarti* are from exposed, wave-washed beaches where the substrate is of sand, rock or shingle. There are, however, a few records from more sheltered beaches and areas, but with one exception (a mud bottom) the substrate was hard, and the depth invariably never more than 30 ft.

Food. Twenty specimens (from 12 localities) were examined. Of these, 17 contained ingested material. One individual contained fish remains (very fragmentary and unidentifiable, even to family) together with a little macerated phanerogam. tissue. Eleven others yielded either macerated plant tissue (f.4), or a mixture of plant tissue and insect fragments (larval Ephemeroptera) ; five specimens contained only fragments of larval Ephemeroptera.

Breeding. Little information is available on reproduction in this species. Fishes less than 95 mm. S.L. are immature, as is one larger specimen (a male, 100 mm. S.L.). The largest fish (156 mm. S.L.) is a male.

Affinities. Superficially, *H. paraguiarti* resembles *H. guiarti* both morphologically and trophically, although *H. guiarti* apparently includes a greater proportion of fish in its diet. Morphologically the species may be distinguished by the straight dorsal head profile of *H. paraguiarti* (gently curved in *H. guiarti*), its longer head (33·0–36·8, M = 34·8 per cent standard length *cf.* 29·5–33·8, M = 31·4 per cent), somewhat broader snout, and fewer, coarser outer teeth (42–60, M = 53, *cf.* 48–74, M = 62 is the upper jaw). Live colours are unknown for *H. paraguiarti*, but the coloration of preserved, sexually active males is noticeably darker than that of *H. guiarti* males. Osteological differences, especially in neurocranial shape, are discussed above (p. 70).

Haplochromis paraguiarti also resembles, rather closely, *H. acidens*; the species are compared on p. 76.

Some specimens of *H. prognathus*, a rather variable species, resemble *H. paraguiarti* but there are several differences which serve to distinguish even these superficially similar individuals; *H. paraguiarti* has a shorter head (33·0–36·8, M = 34·8 per cent of standard length, *cf.* 35·5–38·4, M = 36·9 per cent), a shallower preorbital (14·5–19·5, M = 16·9 per cent head, *cf.* 18·8–23·1, M = 20·8 per cent), shorter snout (31·0–36·2, M = 33·5 per cent head, *cf.* 33·4–39·0, M = 37·0 per cent), and a larger eye (23·8–28·6, M = 26·2 per cent head, *cf.* 20·0–25·0, M = 22·6 per cent). Differences in neurocranial form between the species are also distinctive, although the neurocranium of *H. paraguiarti* is intermediate between the more generalized *H. guiarti* type and the relatively elongate skull of *H. prognathus* (see p. 111).

When all characters are considered, *H. paraguiarti*, despite its superficial resemblance to *H. guiarti*, is probably more closely related to *H. prognathus*. It appears to possess the structural characters of the ancestral species or species group from which piscivorous predators like *H. prognathus*, *H. bartoni* and *H. mandibularis* were derived. Outside the piscivorous predator group, it shows very close relationship with *H. acidens* (see p. 76).

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.) 1966.3.9.324	Beach near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.6 (Holotype)	Beach near Nasu Point (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.338–344	Beach near Nasu Point	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.313–314	Fisherman's point near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.320–323	Near Grant Bay	E.A.F.R.O.
B.M. (B.H.) 1966.3.9.333–337	Entebbe Harbour	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.317–319	Buka Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.312	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.325–330	Beach near Hannington Bay	E.A.F.R.O.
	Kenya	
B.M. (N.H.) 1966.3.9.316	Kamaringa (Kavirondo Gulf)	E.A.F.R.O.
	Tanzania	
B.M. (N.H.) 1966.3.9.311	Beach N. of Majita	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.315	Majita Beach	E.A.F.R.O.
	Lake Victoria	
B.M. (N.H.) 1966.3.9.331–332	Locality unknown	E.A.F.R.O.

Haplochromis acidens sp. nov.

(Text-fig. 13)

Haplochromis percoides (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 296 (specimens from Kakindu, Victoria Nile, B.M. [N.H.] reg. no. 1911.3.3.82–3).

Paratilapia serranus (part): Boulenger, 1915, *op. cit., tom. cit.*, 334 (specimens from Ripon Falls, nr. Jinja, B.M. [N.H.] reg. no. 1911.3.3.20–1).

Haplochromis nigrescens (part): Regan, 1922, *Proc. zool. Soc. Londn.*, 172 (excluding his tentative synonymy of *Astatotilapia roberti* Pellegrin, and the synonymy of *Paratilapia parvidens* Blgr., for which see Greenwood, 1959, p. 194).

NOTES ON SYNONYMY. It is obvious that Regan's (1922) redescription of *H. nigrescens* (Pellegrin), 1909 was influenced by Pellegrin's figure of that species (Pellegrin, 1910, *Mem. soc. Zool. France*, 32, pl. 14, fig. 3). The fish depicted certainly does resemble a specimen of the species here described as *H. acidens*, but the type specimen of Pellegrin's *Astatotilapia nigrescens* more closely resembles *Haplochromis flavipinnis* (personal observations). Boulenger (1915) actually synonymized *A. nigrescens* Pellegrin with *H. percoides* Blgr., 1906 but this action was unacceptable to Regan, who resurrected the species as *Haplochromis nigrescens*. Certainly there are similarities between *A. nigrescens* type specimen and *H. percoides*, but my study of the type was revealed several differences (see appendix for a re-description of this specimen and further comments on its affinities).

In earlier papers I had accepted Regan's resurrection of *H. nigrescens*, and used specimens identified by him as a basis for comparing other Lake Victoria species with *H. nigrescens*; thus, where *H. nigrescens* is mentioned in those papers, the name should now be corrected to read *H. acidens*.

Two of the three Lake Victoria specimens examined by Regan undoubtedly can be referred to *H. acidens*, but I am uncertain about the identity of the third fish. It is the smallest specimen, and because so little is known about small fishes of this and related groups, diagnostic characters applicable to larger individuals cannot be used with confidence. In many respects, this specimen resembles larger individuals of *H. prognathus*.

HOLOTYPE: an adult male, 108 mm. standard length, from Kisumu Kavirondo Gulf (Kenya), B.M. (N.H.) reg. no. 1966.2.21.1. Named *acidens* from its sharp, needle-like teeth.

DESCRIPTION: based on 17 specimens 67–128 mm. S.L., including the holotype and two of the specimens examined by Regan (B.M. [N.H.] reg. no. 1911.3.3.20–1).

Depth of body 34·6–40·3 (M = 38·1) per cent of standard length, length of head 34·0–36·7 (M = 35·4) per cent. Dorsal head profile gently concave (clearly so in most specimens but weakly concave in a few), sloping fairly steeply; premaxillary pedicels not prominent.

Preorbital depth 15·2–19·2 (M = 17·1) per cent of head, least interorbital width 21·4–28·2 (M = 24·5) per cent. Snout as long as broad or 1·1–1·2 times longer, its length 31·8–37·2 (M = 34·2) per cent of head, eye diameter 23·0–29·0 (M = 26·4), depth of cheek 23·0–28·2 (M = 25·7) per cent.

Caudal peduncle 14·8–17·9 (M = 16·6) per cent of standard length, 1·1–1·5 (mode 1·3) times as long as deep.

Mouth slightly oblique, lips somewhat thickened, premaxilla with a slight median expansion. Jaws equal anteriorly, the lower 44·0–50·2 (M = 46·9) per cent of head, 1·9–2·4 (rare), mode 2·1, times as long as broad. Posterior tip of the maxilla reaching the vertical through the anterior orbital margin, occasionally not quite reaching this point.

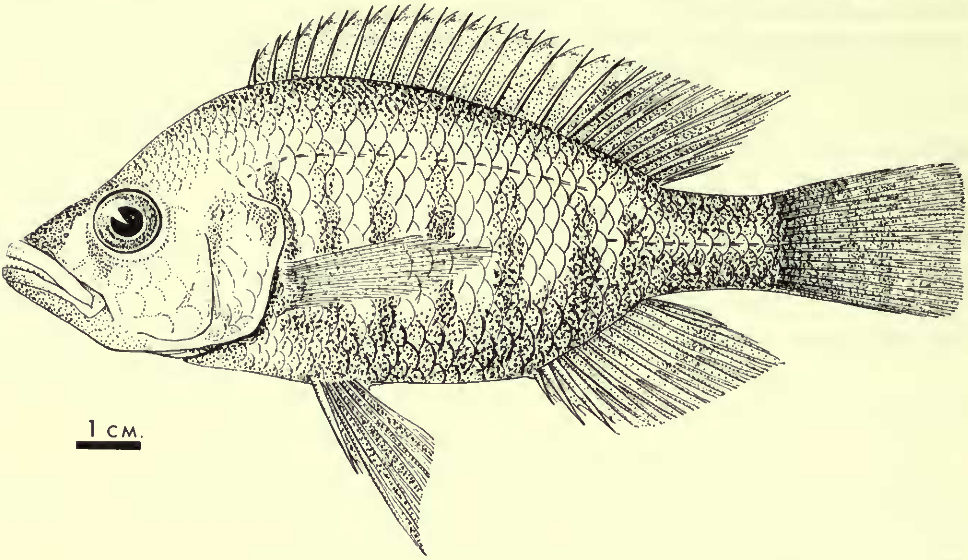

FIG. 13. *Haplochromis acidens.* Drawn by Barbara Williams.

Gill rakers : moderately slender to slender, the lower 1–4 reduced, the upper 3 or 4 flattened and lobed in some fishes ; 10 (rarely 9 or 11) on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 (f.1), 32 (f.8), 33 (f.7) or 34 (f.1), cheek with 3 (rarely 4) rows. Five and a half to 7 (mode 6) scales between the dorsal fin origin and the upper lateral line, 5 or 6 (mode), rarely 6½ or 7 between the pectoral and pelvic fin bases.

Fins : Dorsal with 23 (f.1), 24 (f.7) or 25 (f.9) rays, comprising 15 (f.12) or 16 (f.5) spinous and 7 (f.1), 9 (f.11) or 10 (f.5) branched rays. Anal with 11 (f.7) or 12 (f.10) rays comprising 3 spines and 8 or 9 branched elements. Pectoral 22·7–28·0 (M = 24·9) per cent of standard length. Pelvics with the first two branched rays slightly produced, relatively more so in adult males. Caudal truncate to subtruncate, scaled on its proximal half to two-thirds.

Teeth. In the outer row of both jaws the teeth are tall, slender and slightly curved. Fishes between 67 and 90 mm. S.L. have unicuspid teeth anteriorly, and weakly bicuspid teeth laterally and posterolaterally. Larger fishes have only unicuspids in the outer row. The anterior teeth in the upper jaw of the largest specimens may be relatively enlarged (*i.e.* stouter and longer than the lateral teeth). There are 40–64 (M = 48) teeth in the outer, upper row.

The inner rows of the upper jaw are composed of tricuspid teeth in fishes < 90 mm. S.L. and a mixture of uni- and tricuspids in larger fishes; there is an increased proportion of unicuspids in specimens > 115 mm. S.L. In fishes over 100 mm. S.L. the outermost row of the inner series is often composed of unicuspids and the remaining rows of tricuspids. The inner rows are widely spaced in most fishes so that the teeth form a broad band anteriorly and anterolaterally. There are 3 or 4 rows of teeth in the upper jaw.

In the lower jaw of most specimens less than 120 mm. S.L., only tricuspid teeth are found, but some unicuspids also occur in fishes of this size group. Larger individuals have a mixture of tri- and unicuspid or tri- and weakly tricuspid teeth; only rarely are all the lower, inner teeth unicuspid. There are 2 (mode) or 3 rows of inner teeth in this jaw.

Osteology. The neurocranium of *H. acidens* departs from that of *H. guiarti* towards the *H. mento* type (see Greenwood, 1962). The slope of its anterior dorsal profile (from vomer tip to the origin of the supraoccipital crest) is less steep than in *H. guiarti*, and the maximum width (across the otic region) is relatively less, as is its greatest depth (exclusive of the supraoccipital crest). In all these characters, *H. acidens* is intermediate between *H. guiarti* and *H. prognathus*, a species whose neurocranium could provide a basic " bauplan " from which the more extreme " *mento* "-type evolved.

The premaxilla is somewhat beaked, with the dentigerous surface expanded and protracted medially; the pedicels are elongate, being almost as long as the horizontal arms of the bone.

The lower pharyngeal bone is fine, and has the dentigerous surface broader than long. Lower pharyngeal teeth are arranged in 24–28 rows, and are slender, compressed and distinctly cuspidate, with those in the two median rows somewhat coarser than the others.

Vertebral counts from 12 specimens are: $13 + 16$ (f.4), $13 + 17$ (f.7) and $14 + 16$ (f.1), giving totals of 29 and 30.

Coloration. Live colours : Males (sexually active) have a slatey-blue ground colour, darkest dorsally. Dorsal fin smokey-grey with a pale red margin and a deep red flush on the soft part. Caudal dark grey with deep red streaks between the rays. Anal dark hyaline with a dull maroon flush, and orange-red ocelli. Pelvics black.

Females (adult and quiescent) : dorsal surface yellowish-grey shading to silver on the flanks and belly. Dorsal fin hyaline but with a yellowish base. Anal and caudal dark hyaline. Pelvics hyaline.

Preserved material : Males (adult and sexually active) : ground colour brown (darker than in females and juveniles), darkest dorsally and on chest, belly and ventral half of the caudal peduncle; six to eight vertical bands cross the flanks and caudal peduncle, each band broadening slightly below the level of the upper lateral line, and merging ventrally with the dark body coloration, but remaining discrete dorsally. A narrow, dark lachrymal stripe runs from the anterior border of the eye, sloping backwards to pass behind the posterior tip of the maxilla; a dark narrow stripe outlines the vertical limb of the preoperculum. The spinous dorsal is greyish, the soft part darker on its basal two-thirds, maculate over the posterior half. Caudal maculate on its proximal half to two-thirds. Pelvics dusky, particularly on the basal half; membrane covering the spine colourless. Anal greyish to hyaline, with two, ill-defined and dark grey to dusky ocelli.

Males (*sexually quiescent*) *:* as above but all stripes and bars are much fainter and less well-defined, and the ventral body surface is not noticeably darker than the dorsum, although still darker than the mid-flank region. Only the basal half of each pelvic fin is dusky, and the anal ocelli are almost invisible.

Immature fishes have the same coloration as females.

Ecology. Habitat. The majority of specimens is from a sheltered habitat in the Kavirondo Gulf near Kisumu. At this place the water was about 10 ft. deep, and the substrate of mud; fairly dense stands of submerged plants were common in the area. The other specimens are recorded as being from " Jinja, Ripon Falls ". I am presuming that this locality is in the Napoleon Gulf, that is, above the falls. The area, before the submergence of the Falls, was sheltered, with a hard substrate and, at least close inshore, fairly dense plant stands.

Food. All sixteen specimens examined came from the Kisumu locality, but were caught on different occasions; fifteen specimens contained ingested material in the stomach and intestines. Every gut had, as its major content, finely macerated phanerogam tissue and varying amounts of epiphytic diatoms. Some specimens also contained a flocculent, grey-green mass (as seen in preserved material) thought to be bottom debris, principally blue-green algae. In addition, one gut yielded a few fish bones, one a number of insect eggs (apparently undigested), one a mass of tissue (thought to be the foot of a gastropod) and some fragments of larval Ephemeroptera, and another, fragments of unidentifiable insects.

The phanerogam tissue is very finely divided, and a larger proportion seems to be digested than is the case in other phytophagous species examined.

The apparently vegetarian diet of *H. acidens* is at variance with the dentition and general facies which are essentially those of a piscivorous predator. The length of the gut ($1\frac{1}{2}$ to 2 times standard length) is greater than in the piscivores, but is not as long as the gut in purely phytophagous species.

Breeding. Specimens $<$ 90 mm. S.L. are immature; both sexes reach the same maximum adult size.

Affinities. In its general appearance, *H. acidens* resembles a number of the deeper-bodied piscivorous species, and one of the specialized predators on larval and embryo fishes, *H. parvidens* (Greenwood, 1959).

Perhaps the greatest resemblance is between *H. acidens* and *H. paraguiarti.* Both species have similar neurocrania and jaw structure, but *H. acidens* has finer teeth, a deeper body (34·6–40·3, M = 38·1 per cent of standard length, *cf.* 31·7–36·6, M = 34·8%) and a concave as opposed to a straight dorsal head profile.

Also showing an overall similarity with *H. acidens* is *H. maculipinna.* The concavity of the dorsal head profile in *H. acidens* again serves as one differentiating character. Others are its less oblique jaws, fewer (40–64, M = 48 *cf.* 50–80, M = 62), more slender and longer teeth, and its larger chest scales (5–6 between pectoral and pelvic fin bases, *cf.* 6–9, mode 7 or 8, in *H. maculipinna*). The neurocrania of the two species also differ, that of *H. maculipinna* being deeper and having a steeper dorsal profile ; the premaxilla in this species lacks a pronounced median expansion, and the pedicels meet the horizontal arms almost at right angles (and not at the more acute angle found in *H. acidens*).

From other species of the *H. serranus* group (*H. victorianus*, *H. serranus*, *H. spekii* and *H. nyanzae*), *H. acidens* is distinguished by its concave dorsal head profile, smaller eye, finer, longer and fewer teeth (at least as shown by the mean number, the ranges overlap), less oblique and non-prognathous lower jaw, and by the absence of a prominent mental bump at the symphysis of the dentaries. Other differences also serve to distinguish *H. acidens* from individual species of the *H. serranus* complex ; for these see the species descriptions in Greenwood (1962) and p. 32 above for *H. spekii*.

At about the same level of similarity with *H. acidens* is *H. prognathus*. This species differs from *H. acidens* chiefly in its shallower body (30·1–37·1, M = 33·3% of standard length, *cf.* 34·6–40·3, M = 38·1%), deeper preorbital (18·8–23·1, M = 20·8% of head, *cf.* 15·2–19·2, M = 17·1%) and smaller eye (20·0–25·0, M = 22·6% of head, *cf.* 23·0–29·0, M = 26·4%). The dentition and neurocrania of the species differ quite markedly, with *H. prognathus* having a skull nearer the *H. mento* type (see Greenwood, 1962, and p. 81) and stouter teeth.

It is difficult to assess the phyletic position of *H. acidens*. The level of anatomical specialization, especially of the syncranium and dentition, suggests affinity both with the *H. serranus* species group and with *H. prognathus*, a species not far removed from that group but probably representative of the ancestral type from which such specialized forms as *H. mento* and *H. macrognathus* evolved. Its plant diet suggests a possible trophic specialization paralleling that achieved by a species (*H. phytophagus*) related to the small, anatomically generalized, and usually insectivorous species (Greenwood, 1966).

In an earlier paper (Greenwood, 1959), I suggested that *H. parvidens* might have evolved from a species anatomically like *H. acidens* (called *H. nigrescens* in that paper) ; this relationship is discussed further on page 114.

Phyletically, *H. acidens* was probably derived from the same stem as *H. paraguiarti* ; this stem could have been related to either an *H. guiarti*-like lineage, or to an *H. serranus*-like one.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1911.3.3.20–21	Jinja, Ripon Falls . . .	Bayon
	KENYA	
B.M. (N.H.) 1966.3.9.107–121	Kavirondo Gulf, near Kisumu .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.1 (Holotype)	Kavirondo Gulf, near Kisumu .	E.A.F.R.O.

Haplochromis prognathus (Pellegrin), 1904

(Text-figs. 14 and 15)

Paratilapia prognatha Pellegrin, 1904 (probably in part; the identity of the three smallest syntypes is still in doubt), *Bull. Soc. Zool. France*, **29**, 185; *Idem*, 1905, *Mem. Soc. Zool. France*, **17**, 181, pl. 16, fig. 4. Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 333, fig. 224 (in part, the syntype B.M. [N.H.] reg. no. 1905.2.28.1, *ex* Kavirondo Gulf).

Pelmatochromis spekii (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 417.

Haplochromis prognathus: Regan, 1922, *Proc. zool. Soc. London*, 177.

Haplochromis taeniatus Regan, 1922, *op. cit.*, 170, text-fig. 3.

Haplochromis macrodon Regan, 1922, *op. cit.*, 176, text-fig. 4.

Haplochromis lamprogenys Fowler, 1936 *Proc. Acad. Nat. Sci. Philad*, ***88***, 330, fig 137.

Haplochromis steindachneri Lohberger, 1929. *Anz. Akad. Wiss. Wein*, no. 17, 207.

Haplochromis versluysi Lohberger, 1929, *Anz. Akad. Wiss. Wein* no. 17, 206.

Haplochromis rebeli Lohberger, 1929, *Anz. Akad. Wiss. Wein.*, no. 11, 94 (probably in part; the identity of one paratype, a female 116 mm. S.L., reg. no. 18768 of the Vienna Museum, is still doubtful).

LECTOTYPE: a fish 136·0 mm. standard length, B.M. (N.H.) reg. no. 1905.2.28.1 (presented by the Paris Museum), collected by C. Alluaud from Kavirondo Bay, Kenya. This specimen appears to be the fish figured by Pellegrin (1905), and is chosen as lectotype principally for that reason.

Note: Defining this species has proved particularly difficult, mainly because of the condsiderable intraspecific variability in head shape (see text-fig. 15). This variability, although apparent to the eye, is not readily quantifiable. Intergrades exist between the most outstanding variants, and now that a large series of specimens is available it appears that the variation is, to a large extent, size correlated. In fishes less than 110 mm. S.L., the snout seems protracted and the dorsal head profile has a marked and extended concavity above the eye. In larger fishes the elongate " face " is less noticeable, and the dorsal profile is straighter and slopes steeply (but still with a slight supraorbital concavity).

DESCRIPTION: based on 43 specimens, 70–141 mm. S.L., and including the lectotype, the syntypes of *H. taeniatus* and *H. macrodon* and the holotypes of *H. steindachneri* and *H. lamprogenys*. The types of *H. rebeli* and *H. versluysi* were examined but are not included in this redescription.

Depth of body 30·1–37·1 (M = 33·3) per cent of standard length, length of head 35·3–38·4 (M = 36·9) per cent; head profile variable (see note above), usually with a supraorbital concavity, the dorsal outline sloping at an angle of 30°–40° with the horizontal.

Preorbital depth 18·8–23·1 (M = 20·8) per cent of head, least interorbital width 18·1–23·7 (M = 21·0) per cent. Snout length 33·4–39·6 (M = 37·0) per cent of head, $1\frac{1}{4}$ to $1\frac{1}{3}$ times as long as broad (rarely $1\frac{3}{8}$ times). Eye diameter with slight negative allometry, 20·0–25·0 (M = 22·6) per cent of head; in fishes 70–90 mm. S.L., the eye is clearly larger than the cheek is deep but in specimens 90–110 mm. it is equal to or slightly smaller than the cheek, a relationship that holds for some larger individuals (110–125 mm. S.L.) although in most individuals in this size range the eye diameter is manifestly less than the cheek depth. Depth of cheek 20·6–28·6 (M = 24·5) per cent of head (18·9% in the smallest specimen).

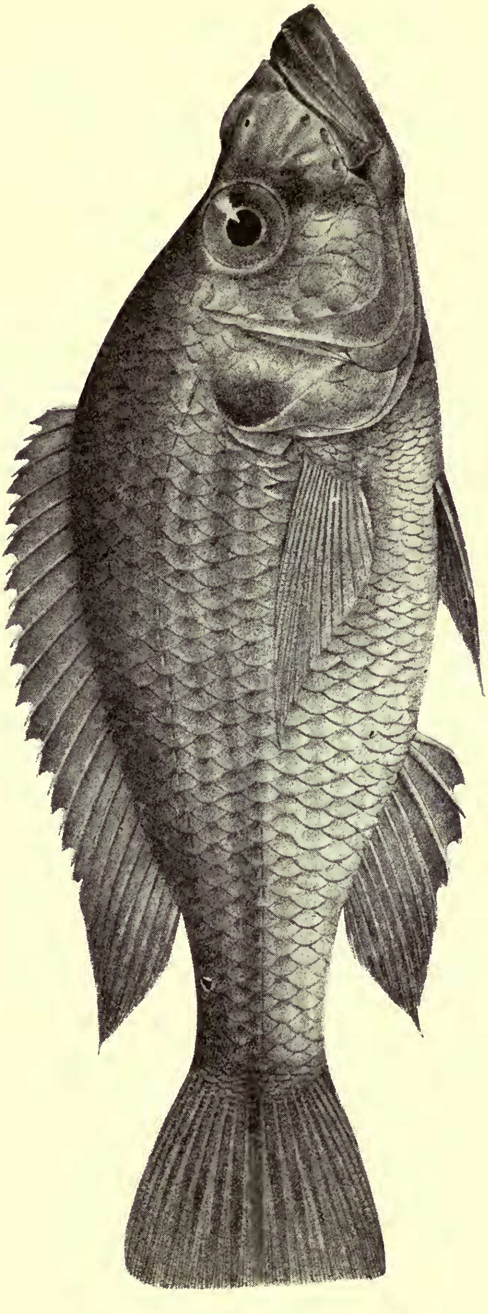

FIG. 14. *Haplochromis prognathus*. Lectotype, about natural size. From Boulenger, *Fishes of the Nile.*

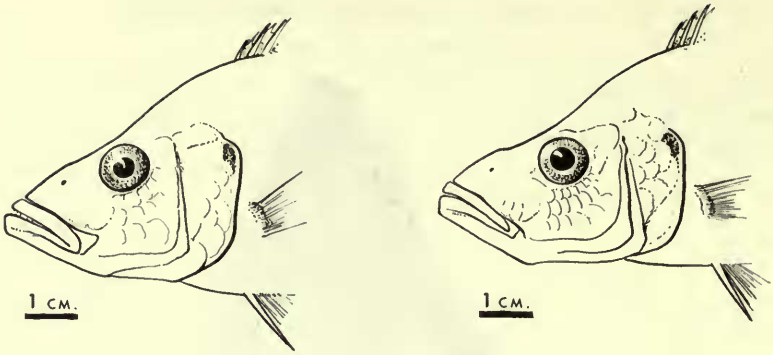

FIG. 15. *Haplochromis prognathus*, showing variability of head profile.

Caudal peduncle 14·6–19·0 (M = 16·0) per cent of standard length, 1·2 (rarely)–1·7 times is long as deep (modal range 1·3–1·5).

Mouth moderately oblique, the jaws equal anteriorly or the lower projecting slightly; lower jaw with a slight mental protuberance, its length 42·5–51·1 (M = 46·2) per cent of head, 2·0–2·8 (mode 2·4) times as long as broad. Posterior tip of the maxilla not reaching the vertical through the anterior orbital margin (except in one specimen), but usually reaching a point nearer this line than one through the nostril.

Gill rakers: 8–10 (mode 9) on the lower part of the first gill arch, the lower 1–3 rakers reduced, the upper 3 or 4 often flat or flat and lobed, the remainder slender.

Scales: ctenoid. Lateral line with 30 (f.2), 31 (f.12), 32 (f.21) or 33 (f.8) scales; some individuals lack pores in the scales of this series. Cheek with 3 (occasionally 4) rows. Five to 7 (mode 6) scales between the dorsal fin origin and the upper lateral line, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 23 (f.6), 24 (f.26) or 25 (f.10) rays, comprising 14 (f.11), 15 (f.28) or 16 (f.3) spines and 8 (f.1), 9 (f.28) or 10 (f.13) branched rays. Anal with 11 (f.2), 12 (f.21) or 13 (f.11) rays, comprising 3 spines and 8 (f.2), 9 (f.21) or 10 (f.11) branched elements. Pectoral fin shorter than head, 22·0–29·3 (M = 25·7) per cent of standard length. First pelvic branched ray slightly produced in both sexes but proportionately more so in males. Caudal truncate or subtruncate, scaled on its basal half to two-thirds.

Teeth. In the smallest fish examined (70 mm. S.L.) the outer teeth in both jaws are mostly unequally bicuspid, but a few unicuspids are present. Fishes between this size and 105 mm. S.L. have mostly unicuspids in the outer row, but some bicuspids occur posterolaterally in the upper jaw. Fishes > 105 mm. have only unicuspid outer teeth, a condition found occasionally in individuals as small as 90 mm. S.L. The unicuspids are slightly curved inwards, and vary in form from relatively slender to moderately stout. There are 30–60 (M = 45) teeth in the outer row of the upper jaw, the number not showing any correlation with the fish's size. Regan's (1922) " key " character separating *H. taeniatus* from *H. macrodon* (outer teeth numerous, close together *cf.* outer teeth rather strong, set well apart) is hardly trenchant even when only the type specimens are compared, and is inapplicable when a large series is examined.

The inner teeth are mostly tricuspids in fishes < 110 mm. S.L., but an admixture of tri- and unicuspids (or weakly tricuspids) is found in fishes at the upper end of this size range. Some tricuspids also occur in large fishes, but in the majority of these all inner rows are composed of unicuspids. When tri- and unicuspids occur together in fishes > 120 mm. S.L. the tricuspids are confined to the innermost rows. Inner teeth are arranged in 2 (mode) or 3, rarely 1, rows in the upper jaw, and in 1 (mode) or 2 (rarely 3) rows in the lower.

Osteology. The neurocranium of *H. prognathus* is approximately intermediate between that of *H. paraguiarti* and *H. mento* (see p. 70, and Greenwood, 1962). It thus closely resembles the neurocrania of *H. bartoni*, *H. mandibularis*, *H. argenteus* and *H. longirostris* (see p. 112 and Greenwood, *op. cit*), in Lake Victoria, and *H. venator* in Lake Nabugabo (Greenwood, 1965). From the four former species it differs most noticeably in its deeper supraoccipital crest, and from *H. argenteus* also by its being somewhat broader anterior to the orbits. There are also resemblances in neurocranial form between *H. prognathus* and *H. xenostoma* (see p. 53) but the differences here are somewhat more pronounced than in the other species mentioned.

The premaxilla has an expanded median dentigerous surface which gives the bone a beaked appearance ; this is a feature of those piscivorous species which I consider to be more specialized in body-form than the members of the *H. guiarti* and *H. serranus* species complexes (see Greenwood, 1962). In contrast, the dentary of *H. prognathus* is of the stout, deep-bodied type found in the latter groups.

The lower pharyngeal bone is triangular, with the dentigerous surface as long as broad or slightly broader (both conditions are of equal frequency). The lower pharyngeal teeth are fairly coarse, with cylindrical necks and compressed, weakly bicuspid crowns ; these teeth are well-spaced on the bone in 18–24 rows.

Vertebral counts in 8 specimens are : 12 + 17 (f.2), 13 + 15 (f.1), 13 + 16 (f.4) and 13 + 17 (f.1) giving totals of 28–30.

Coloration. Live colours are unknown. *Preserved material : Males* (*adult and sexually active*). Body and head brownish above the midline, silvery-yellow below ; two faint lateral bands are visible, one running midlaterally from behind the eye to the origin of the caudal fin, the other along the upper lateral line. There is a faint, ill-defined but broad lachrymal band, but it does not extend ventrally to the margin of the preorbital. Dorsal fin greyish, the dark pigment most intense basally on the spinous region, lappets dusky ; soft dorsal maculate. Caudal dark grey, darkest between the rays on the proximal two-thirds of the fin. Anal greyish, lappets black, as may be the basal part of the membrane between the spines ; 2 or 3 large but faint, greyish ocelli. Pelvics black.

Females (*adult and juvenile*). Light grey-brown above, silvery below ; very faint traces of longitudinal bands as in males, the lower often visible on the posterior third of the body. All fins hyaline, but the caudal is dark on its proximal two-thirds.

Ecology. Habitat. Haplochromis prognathus is apparently confined to water less than 20 ft. deep, and to hard substrates ; it occurs in both sheltered and exposed localities, including wave-washed beaches.

Food. Of the 33 specimens examined (from 11 localities), 22 contained food. Ten specimens contained only remains of fishes (predominantly small Cyprinidae, but *Haplochromis* were also identified), 3 yielded fish and insect remains (the fish unidentifiable, the insects adult Isoptera and larval Ephemeroptera), 7 contained only insects (adult Isoptera and larval Ephemeroptera), 1 contained unidentifiable fish remains and some plant fragments (undigested), and 2 specimens contained unidentifiable material (? bottom debris) and some plant remains.

Breeding. Little is known about the breeding habits of this species ; no brooding individuals have been recorded. Sexual maturity is attained at a length of about 100 mm., but larger juvenile individuals (up to 120 mm.) are known. Both sexes reach the same maximum adult size.

Affinities. There is nothing particularly outstanding about the general appearance of *H. prognathus* when it is compared with the other relatively deep-bodied predatory species of Lake Victoria. Thus, it bears a superficial resemblance to several piscivorous species, especially *H. serranus*, *H. bartoni*, *H. nyanzae* and *H. mandibularis*.

From *H. serranus*, *H. prognathus* differs in its slightly shallower body (30·1–37·1, M = 33·3% standard length *cf.* 32·7–39·2, M = 36·0%), deeper preorbital (18·8–23·1, M = 20·8% head, *cf.* 14·6–20·0, M = 17·7%), slightly longer snout (33·4–39·0, M = 37·0% head, *cf.* 30·8–37·0, M = 34·0%), shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 47·0–60·0, M = 54·3%) and slightly larger chest scales (5–7, mode 6, between the pelvic and pectoral fin bases, *cf.* 7 or 8 [rarely 6]). The preserved coloration of the two species suggests a fairly marked difference in live colours, and there are clear-cut differences in neurocranial form (see p. 110).

From *H. bartoni* (probably its nearest extant relative), *H. prognathus* differs in having a broader and shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 50·8–57·0, M = 52·5%), fewer outer teeth in the upper jaw (30–60, M = 45, *cf.* 50–80, M = 62), the maxilla not extending so far posteriorly (reaching or almost reaching the orbit in *H. bartoni*), and its smaller chest scales. Neurocranial form in the two species is similar.

The characters separating *H. prognathus* from *H. nyanzae* are its longer snout (33·4–39·6, M = 37·0% head, *cf.* 33·4–35·8, M = 34·5%), more oblique lower jaw, its maxilla not reaching the orbit, and its larger chest scales. Unfortunately it has not been possible to compare directly the neurocrania of the two species. But, from radiographs it seems probable that the skull of *H. nyanzae* is like that of *H. serranus* (see Greenwood, 1962).

Haplochromis prognathus differs from *H. mandibularis* in having a broader snout, shorter lower jaw (42·5–51·1, M = 46·2% head, *cf.* 47·3–56·8, M = 51·5%), and longer caudal peduncle (14·6–19·0, M = 16·6% standard length, *cf.* 12·2–15·2, M = 14·2%). Neurocranial form in the two species is similar.

Haplochromis prognathus is, apparently, closely related to *H. argenteus*. At first sight, the great variability in head shape of *H. prognathus* obscures the relationship. But, if smaller specimens of *H. prognathus* are compared with larger individuals of *H. argenteus* the likeness is striking. Morphometrically, even superficially dissimilar specimens of the two species are not readily separable. Characteristics of the lower jaw serve to distinguish the species. The lower jaw of *H. prognathus* is broader (length/breadth ratio 2·0–2·8 [modal range 2·0–2·4], *cf.* 2·3–3·1 [modal range 2·8–3·0]), shorter (42·5–51·1, M = 46·2% of head, *cf.* 45·0–59·0, M = 50·2%), less oblique and less prognathous.

The possible phyletic relationship of *H. prognathus* within the Lake Victoria species-flock will be discussed later (p. 110) ; outside Lake Victoria, *H. prognathus* is probably related to *H. venator* of Lake Nabugabo (Greenwood, 1965). Indeed *H. venator* could well have been derived from populations of *H. prognathus* cut off when the sand bar which isolated Lake Nabugabo was formed about 4,000 years ago.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.304 (Syntype *H. macrodon*)	Entebbe	Degen
B.M. (N.H.) 1906.5.30.305–6 (Syntypes *H. macrodon*)	Bugonga	Degen
B.M. (N.H.) 1906.5.30.250 (Syntype *H. taeniatus*)	Entebbe	Degen
B.M. (N.H.) 1966.3.9.50	Entebbe, Airport Beach	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.64–65	Napoleon Gulf, near Jinja	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.53–59, 66–67, 72–75	Beach near Nasu Point (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.68–71	Katebo	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.79–83	Bugonga, near Entebbe	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.51–52	Kagera Bay, near mouth of Kagera River	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.60–63	Bukafu Bay	E.A.F.R.O.
Vienna Museum 17872 (Type of *H. steindachneri*)	Sesse Islands	Rolle
Academy of Nat. Sciences Philadelphia ANSP 66131 (Holotype of *H. lamprogenys*)	Kitala	——
	KEYNA	
B.M. (N.H.) 1905.2.28.1 (Lectotype)	Kavirondo Gulf	Alluaud
B.M. (N.H.) 1905.12.11.4 (Syntype *H. taeniatus*)	Kavirondo Gulf	Alluaud
	TANZANIA	
B.M. (N.H.) 1966.3.9.76–78	Mwanza Harbour	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.84	Capri Bay, Mwanza	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1906.5.30.251–2, 256	Locality unknown	Degen
Vienna Museum 17876–7 (Types of *H. versluysi*)	Locality unknown	Rolle
Vienna Museum 18830 (Holotype of *H. rebeli*)	Locality unknown	Rolle
Vienna Museum 18769–71 (Paratypes of *H. rebeli*)	Locality unknown	Rolle

Haplochromis argenteus Regan, 1922

(Text-fig. 16)

Paratilapia longirostris (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 332.
Haplochromis argenteus Regan, 1922, *Proc. zool. Soc. Londn.*, 186, fig. 12.

LECTOTYPE: a juvenile female 114·0 mm. standard length, from Bunjako, Uganda (B.M. [N.H.] reg. no. 1906.5.30.266; the specimen figured by Regan).

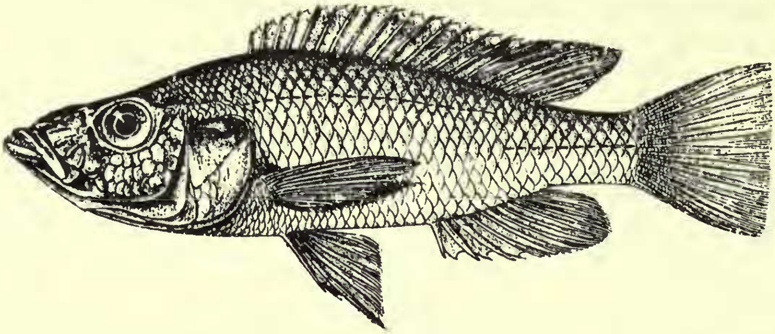

FIG. 16. *Haplochromis argenteus*; the lectotype, a juvenile, about ·75 times natural size. From Regan, *Proc. zool. Soc.*

DESCRIPTION: based on 23 specimens (including the lecto- and paralectotype) 93·0–202·0 mm. standard length.

Depth of body 26·8–34·8 (M = 31·2) per cent of standard length, length of head 35·5–39·6 (M = 36·8) per cent. Dorsal head profile slightly concave, with prominent premaxillary pedicels, and sloping at an angle of 20°–25°.

Preorbital depth 19·6–24·0 (M = 21·7) per cent of head, least interorbital width 17·7–22·3 (M = 20·0) per cent. Snout 1·25–1·40 times as long as broad, its length 34·8–41·6 (M = 37·8) per cent of head, diameter of eye 19·4–23·5 (M = 21·5), depth of cheek 22·3–28·7 (M = 24·7) per cent.

Caudal peduncle 13·5–17·7 (M = 16·1) per cent of standard length, 1·3–1·7 (modal range 1·3–1·5) times as long as deep.

Mouth oblique (35°–40°), the lower jaw projecting moderately in some specimens, its length 45·0–59·0 (M = 50·2) per cent of head, 2·3–3·1 (modal range 2·8–3·0) times as long as broad. Lips slightly thickened. Premaxilla expanded slightly in the midline. Posterior tip of the maxilla reaching a point about midway between the orbit and the nostril, or almost reaching the orbit.

Gill rakers: generally slender but moderately stout in a few fishes; lower 1 or 2 reduced, the upper 3 or 4 (in one fish, the upper 6) flat and lobed. Eight to 10 (mode 9) on the lower part of the first arch.

Scales: ctenoid; lateral line with 29 (f.2), 30 (f.2), 31 (f.5), 32 (f.11), 33 (f.1), 34 (f.1) or 35 (f.1) scales. Cheek with 3 or 4 (rarely 5) rows. Five or 6 (rarely 7) scales between the dorsal fin origin and the upper lateral line, 6 or 7 (less frequently 5) between the pectoral and pelvic fin bases.

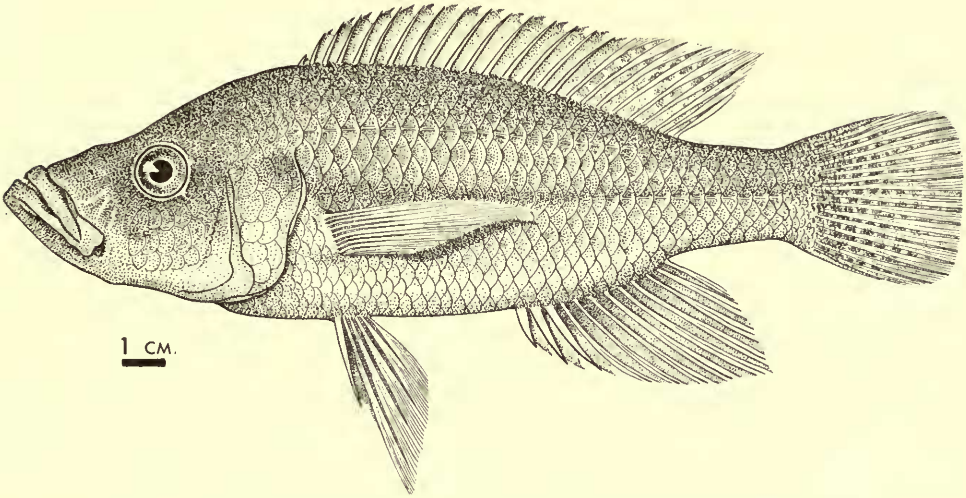

FIG. 16A. *Haplochromis argenteus*, adult. Drawn by Lavinia Beard.

Fins. Dorsal with 23 (f.2), 24 (f.12) or 25 (f.9) rays, comprising 13 (f.1), 14 (f.1), 15 (f.19) or 16 (f.2) spines and 8 (f.2), 9 (f.12) or 10 (f.9) branched rays. Anal with 11 (f.3), 12 (f.19) or 13 (f.1) rays, comprising 3 spines and 8, 9 or 10 rays. Pectoral 24·1–29·7 (M = 25·0) per cent of standard length. Pelvics with the first branched ray somewhat elongate, proportionately more so in adult males. Caudal truncate.

Teeth. Except for the smallest fish examined (the paralectotype 93 mm. S.L.) the outer teeth in both jaws are unicuspid, slender and slightly curved (those situated posterolaterally in the upper jaw more so than the others). In the smallest individual most outer teeth are like those described above but there are also some weakly bicuspid and slender teeth. There are 44–80 (M = 58) teeth in the outer row of the upper jaw, the number showing slight positive correlation with standard length.

In all except four specimens (the two types, 93 and 114 mm. S.L., and two others 88 and 112 mm. S.L.) the inner teeth are unicuspid. Of the exceptional specimens, the largest (lectotype) has an admixture of tri- and unicuspids, the 93 mm. fish (paralectotype) only tricuspids, while the 88 and 112 mm. individuals have tricuspids in the upper jaw and a mixture of tri- and some unicuspids in the lower. Inner teeth are arranged in 2–4 (rarely 5) rows in the upper jaw, and 1–3 in the lower. One exceptional fish (182 mm. S.L.) has a single, irregular row of widely separated teeth in both jaws.

Osteology. The neurocranium of *H. argenteus* is virtually identical with that of *H. longirostris* (see Greenwood, 1962), and also resembles the skull of *H. prognathus.*

The premaxilla is more beaked than that of *H. longirostris.*

The lower pharyngeal bone is narrow, but its dentigerous surface is generally broader than long ; less frequently it is equilateral. The teeth are rather coarse, although they are finer and more compressed in a few fishes. These teeth are arranged in 20–24 (usually 22) rows.

Vertebral counts in 8 specimens are: 12 + 17 (f.3) and 13 + 16 (f.5) giving a total of 29.

Coloration. Live colours are unknown. *Preserved material: Males* (*adult and sexually active*): ground colour grey-silver, darker (almost brown) on back and dorsal head surfaces; tip of lower jaw and anterior part of each ramus dusky. Branchiostegal membrane sooty in the opercular region, dark (but not black) anteriorly. Sub- and interopercula with a golden-yellow flush. An ill-defined to distinct lachrymal stripe runs from the anterior orbital margin to behind the posterior tip of the maxilla. Dorsal fin greyish-yellow, with black lappets, and in some specimens a dusky, irregular banding or marbling on the entire spinous and anterior soft parts. Caudal greyish-yellow, dark grey-brown on the proximal half. Anal greyish with black lappets, and 2 or 3 dead-white ocelli. Pelvics dusky.

Males (*sexually quiescent, and immature*): Ground colours like those of active individuals but somewhat lighter, often with very faint traces of 4 or 5 bars midlaterally on the flanks; the lachrymal stripe is of variable intensity. Dorsal fin as above or without the dark marbling. Other fins also as above, but the anal ocelli may be weakly defined and small, and the pelvics lighter.

Females (*adult and immature*). Ground coloration as in males, but with a faint, interrupted and narrow midlateral band running from the posterior opercular margin to the basal part of the caudal fin. Even fainter traces of a more dorsal longitudinal band (following the course of the upper lateral line) are seen in some specimens; the two bands may be linked by 3 or 4 extremely faint, short and narrow vertical bars. All fins are yellowish, the caudal dark basally.

Ecology. Habitat. Most specimens are from sheltered localities where the bottom is composed of organic mud, and at depths of less than 40 ft. Other localities are, however, more exposed and the substrate is of rock, sand or shingle, but only a few (and juvenile) fishes were obtained from nets operated over exposed beaches.

Food. Of the 20 individuals examined (from 11 localities) 8 had food in the gut. Four fishes contained only insect remains (in 2 thought to be terrestrial species, and in the others identified as larval Ephemeroptera), and 4 had fragmentary fish remains (identified as the cyprinid *Engraulicypris argenteus*).

Breeding. Fishes < 114 mm. S.L. are immature, as is one exceptional specimen of 146 mm. Both sexes reach the same maximum adult size.

Affinities. The species most like *H. argenteus* is *H. longirostris*. There are, however, a number of morphological differences which serve to separate them, including the larger adult size reached by *H. argenteus*. From *H. longirostris*, *H. argenteus* also differs in its less oblique and longer lower jaw (45·0–59·0, M = 50·2% of head, *cf.* 42·2–51·4, M = 46·0%), shorter and deeper caudal peduncle (13·5–17·7, M = 16·1% of standard length, *cf.* 17·2–22·2, M = 19·2%; length/depth ratio 1·3–1·7 [modal range 1·3–1·5], *cf.* 1·7–2·3 [modal range 1·9–2·0]), somewhat deeper body (26·8–34·8, M = 31·2% of standard length, *cf.* 24·6–30·4, M = 27·2%) and slightly longer head (35·5–39·6, M = 36·8% standard length, *cf.* 29·2–36·2, M = 33·0%); also, the premaxilla of *H. argenteus* is somewhat more beaked. In an earlier paper (Greenwood, 1962) I used the ratio of eye diameter to interorbital width as a diagnostic character ; more material of *H. argenteus* has shown, however, that this difference is too slight to be of value.

The similarities between *H. argenteus* and *H. prognathus* are discussed elsewhere (p. 82). When these two species and *H. longirostris* are considered together, it seems probable that *H. argenteus* and *H. longirostris* were derived from an *H. prognathus*-like ancestor, probably as distinct lines developing almost in parallel.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1906.5.30.266 (Lectotype)	Bunjako	Degen
B.M. (N.H.) 1906.5.30.267 (Paralectotype)	Bunjako	Degen
B.M. (N.H.) 1966.3.9.194–195	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.201–202	Pilkington Bay . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.193	Beach near Nasu Point . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.196–198	Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.192	Off S. end of Buvuma Island .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.208–210	Beach near Grant Bay (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.191	Channel between Yempita and Busiri Islands . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.199–200	Kazima Island . . .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.203–204	Off Entebbe Harbour . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.207	Entebbe Harbour . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.205–206	Bukakata Bay	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.90	Locality unknown . . .	Sir. H. Johnston
B.M. (N.H.) 1966.3.9.190	Locality unknown . . .	E.A.F.R.O.

Haplochromis squamulatus Regan, 1922

(Text-fig. 17)

Paratilapia pectoralis (non *Ctenochromis pectoralis* Pfeffer) Boulenger, 1911, *Ann. Mus. Genova* (3), **5**, 66, pl. 1, fig. 2. *Idem*, 1915, *Cat. Afr. Fish*, **3**, 339, fig. 229.

Paratilapia serranus (part) : Boulenger, 1915, op.cit., tom. cit., 334.

Haplochromis guiarti (part): Regan, 1922, *Proc. zool. Soc. Londn.*, 174.

Haplochromis squamulatus Regan, 1922, *op. cit.*, 175 (*nom. nov.* for *Paratilapia pectoralis* Blgr., 1911).

HOLOTYPE : a male (probably adult), 149 mm. standard length, from Jinja (Uganda). Genoa Museum reg. no. C.E. 12977.

DESCRIPTION : based on 54 specimens (including the holotype), 66–198 mm. S.L.

Depth of body 23·5–35·1 (M = 30·3) per cent of standard length, length of head 29·4–39·5 (M = 34·3) per cent. Dorsal head profile moderately to strongly sloping, the premaxillary pedicels prominent and breaking the outline of the profile, snout region sloping at an angle of 40°–50° with the horizontal.

Preorbital depth in fishes < 100 mm. S.L. (N = 11), 12·5–16·5 (M = 15·5) per cent of head, in larger fishes (N = 43) 15·6–21·6 (M = 18·9) per cent, least interorbital width 21·2–28·3 (M = 25·0) per cent. Snout as long as broad to 1·3 times longer, its length in fishes < 100 mm. S.L., 26·0–32·1 (M = 29·1) per cent of head, in larger individuals 20·6–25·9, M = 23·3 per cent. Cheek depth 19·5–29·3 (M = 25·7) per cent of head.

Caudal peduncle 14·3–22·3 (M = 17·9) per cent of standard length, 1·2 (rare)–2·0 (mode 1·7) times as long as deep.

Mouth horizontal or very slightly oblique, jaws equal anteriorly, or infrequently, lower projecting slightly. Length of lower jaw in fishes < 170 mm. S.L. (N = 46), 39·0–48·0 (M = 44·1) per cent of head, 44·2–51·0 (M = 47·5) per cent in larger fishes (N = 8); 1·5–2·5 (mode 1·8, modal range 1·5–2·0) times as long as broad in fishes of all sizes. Posterior tip of the maxilla generally reaching the vertical through the anterior orbital margin or to below the eye, but not reaching either point in a few individuals. Lips slightly thickened; premaxilla not expanded medially.

Gill rakers: short and stout, often flat, in most specimens; in fishes < 120 mm. S.L., but also in a few larger individuals, most of the rakers are relatively slender. Eight–10 (mode 9), rarely 11, on the lower part of the first arch, the lower 1–3 rakers reduced.

Scales: ctenoid. Lateral line with 32 (f.2), 33 (f.12), 34 (f.8), 35 (f.15), 36 (f.10), 37 (f.6) or 38 (f.1). Pore distribution in this series is irregular, with some pore scales occurring in the horizontal row above that in which the majority lies; also, some scales are without pores and are often smaller than those before and behind them. Cheek with 3 (f.8), 4 (f.32), 5 (f.12) or 6 (f.1) rows of scales. Scales on the nape, chest and belly are small; 6 (f.3) 6½ (f.3), 7 (f.11), 7½ (f.5), 8 (f.14) or 9 (f.16) between the

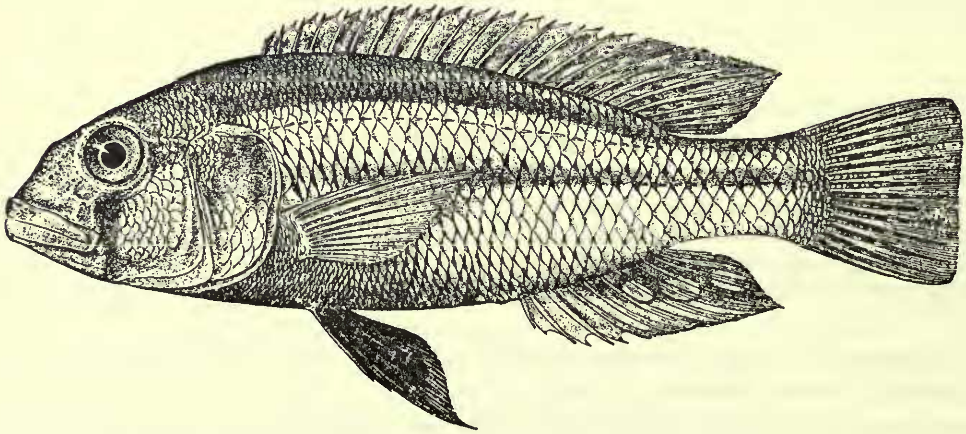

FIG. 17. *Haplochromis squamulatus*, holotype, about ·72 times natural size. From Boulenger, *Cat. Afr. Fish.*

dorsal fin origin and the upper lateral line, 6 (f.1), 7 (f.8), 8 (f.16), 9 (f.25) or 10 (f.3) between the pectoral and pelvic fin bases.

Fins. Dorsal with 24 (f.9), 25 (f.37) or 26 (f.6) rays, comprising 14 (f.2), 15 (f.26) or 16 (f.24) spines, and 8 (f.2), 9 (f.23), 10 (f.25) or 11 (f.2) branched rays. Anal with 11 (f.3), 12 (f.40) or 13 (f.5) rays, comprising 3 spines (except for one specimen with 2), and 8 (f.3), 9 (f.40) or 10 (f.5) branched elements. Pectoral 21·8–27·0 (M = 24·7) per cent of standard length. Pelvics with the first branched ray produced in both sexes but proportionately more so in adult males. Caudal subtruncate to truncate.

Teeth. Most fishes < 105 mm. S.L. have either an admixture of uni- and bicuspid teeth in the outer row of both jaws, or only bicuspids. One specimen (89 mm. S.L.) has predominantly bicuspids and a few tricuspids in the upper jaw, but mostly unicuspids in the lower. In larger fishes of the < 105 mm. group, unicuspid teeth predominate in both jaws, and in fishes > 105 mm. S.L. only unicuspids are found. All outer teeth are relatively slender and gently curved, the unicuspids more so than the bicuspids. The mean number of teeth in the outer row of the upper jaw shows some positive correlation with standard length although there is little difference in the ranges for the various groups ; fishes < 120 mm. S.L. have 50–72, M = 57 teeth in this row, while larger specimens have 52–80, M = 68.

There is less obvious correlation between tooth form and the fish's size when the inner rows of teeth are considered. All fishes < 105 mm. S.L. have only tricuspids in the inner rows. Above this length many fishes have only unicuspids, but a mixture of uni- and tricuspids (or weakly tricuspids) is common even in the largest individuals. Unicuspids occur most frequently in the outer rows of the inner series.

Inner teeth are arranged in 2–6 rows (usually 3 or 4) in the upper jaw, and in 1–6 (usually 2 or 3) in the lower jaw. There is perhaps some correlation between the number of rows and the fish's length because the largest specimens (179–198 mm. S.L.) have the greatest number of inner rows. Also, in larger fishes the inner teeth are implanted very obliquely but are almost vertical in fishes < 105 mm. S.L.

Osteology. The neurocranium of *H. squamulatus* combines characteristics of both the *H. guiarti* and the *H. serranus* types (see Greenwood, 1962). The dorsal preorbital profile rises steeply and is gently curved ; its line is continuous with that of the supraoccipital crest whose anterior point lies further forward than in the skulls of *H. guiarti* and *H. serranus*. In general there is a great similarity between the neurocrania of *H. squamulatus*, *H. michaeli* and *H. martini* (see Greenwood, *op. cit*).

The premaxilla is of the generalized type, and thus lacks a pronounced anterior extension of its medial dentigerous surface.

The lower pharyngeal bone has the dentigerous surface broader than long, from slightly to markedly so. The lower pharyngeal teeth are relatively slender, compressed and distinctly cuspidate ; the teeth are arranged in 22–26 (mode 24) rows.

Vertebral counts in 10 specimens are : 13 + 16 (f.2), 13 + 17 (f.2), 13 + 18 (f.2), 14 + 16 (f.1), 14 + 17 (f.3) giving totals of 29–31.

Coloration. Live colours are known for females (adult) and quiescent males. *Females :* ground colour yellow-silver above shading to yellowish-white ventrally, the dorsal body and head surfaces are darkest. Two distinct longitudinal bands are invariably present, the lower running from the operculum to the caudal fin origin along the level of the lower lateral line, the upper extending from the nape to the end of the dorsal fin at a level about two scale rows below the dorsal fin insertion. Both bands have a finely zig-zagged outline ; the upper band may be faint. Dorsal fin dark neutral. Caudal dark neutral with a yellow flush. Pelvic and anal fins yellow.

Quiescent males have a coloration like that of the females described above.

Preserved material : Males (*adult, sexually active but not ripe*). The general impression is one of dusky greyness, with small areas of light brown on the flanks. The entire head is dark but is lighter on the operculum and lower lip (the lower jaw is dark). A broad black band (faint in some specimens) runs from the posterior opercular margin to the caudal fin origin ; it is crossed by 3 or 4 broad but faint vertical bars in the zone of lighter flank coloration. These bars merge with the dark dorsum and sooty-grey chest and belly. The ventral aspects of the caudal peduncle are also sooty-grey. Dorsal fin yellow-brown with a sooty overlay, the lappets are black, and a few ill-defined dark maculae may be visible on the posterior part of the soft dorsal fin. Caudal dark grey-brown on its proximal three-quarters, yellowish-brown distally. Anal coloured like the dorsal but greyer over the spinous part ; ocelli either not clearly defined, or white with a sooty surround. Pelvic fins dusky over a yellowish ground.

Males (*adult but quiescent*). Ground colour light brown, shading to golden on the ventral surfaces which are, however, overlaid with greyish-black. Dorsal surface of the head and body dark brown. A fairly broad, distinct and almost vertical lachrymal stripe runs from the anteroventral orbital margin to the dentary. A very distinct, broad lateral stripe runs from the opercular margin to the caudal fin base ; the upper margin of this band is irregularly serrate. There are 3 or 4 incomplete but broad and distinct vertical blotches on the ventral half of the flanks, each blotch originating from the midlateral band but not extending to a point more than half way between the lateral band and the ventral body outline. A very faint dark upper lateral band may be distinguished running at a level about midway between the dorsal fin base and the upper lateral line ; this band is often indistinguishable from the generally dark coloration of the dorsum. A third band at the base of the dorsal fin may be visible. Dorsal fin pale brownish-yellow, with a faint sooty overlay ; lappets black, dark blotches present on the soft fin. Anal pale yellowish, with a very faint sooty overlay. Pelvics yellowish with an intense sooty overlay on the anterior half. Caudal dark greyish-yellow.

Immature males are coloured like females (see below),but have a darker ground coloration (almost grey on the chest and belly) and faintly sooty pelvics.

Females (*adult and immature*). Female coloration is very distinctive because of the well-marked lateral bands. The ground coloration is a yellowish-silver, somewhat greyish above the upper lateral line and on the dorsal head surface ; the cheek and operculum are yellow-silver. The midlateral band is black and has characteristically serrate upper and lower margins ; the depth of this band is rather variable in any one fish, and is generally deepest above the anal fin. The upper lateral band also has irregularly serrate margins but it is generally less obvious because of its position on the dark colour of the dorsum. A third longitudinal band, narrower and interrupted, lies along the base of the dorsal fin as a series of narrow, elongate blotches. Dorsal fin yellowish with a faint sooty overlay, and sooty lappets; the soft part often has dark spots and blotches between the rays. Caudal yellowish with dark maculae on the proximal quarter to third. Anal and pelvic fins yellow.

Ecology. Habitat. The species is known from a wide variety of habitats, including sheltered bays and gulfs, exposed beaches, and from certain off-shore localities near small islands. In most places the substrate is hard (rock, sand or shingle) but *H. squamulatus* is known to occur over mud bottoms.

Food. Thirty-six specimens were examined (covering the entire size-range, and from 18 localities); of these, 19 contained food in the gut. In 16 fishes the food consisted entirely of fishes, the remains so macerated that certain identification was difficult; in two cases the remains were identified as *Haplochromis* species, in one as *Engraulicypris*, and in another as a cichlid. In two female fishes the stomach contained many small embryos of cichlid fishes; these could well be the fishes' own broods swallowed at the time of capture, although it is not known whether *H. squamulatus* is a mouth-brooder. A third female fish had several small post-larval cichlids in the stomach; judging from the gonad state of the predator it seems unlikely that the larvae were its own brood.

In addition to the sixteen piscivorous fishes, one other yielded only crustacean remains, one several insect egg-masses, and a third the remains of boring mayfly larvae (*Povilla adusta*).

Breeding. All specimens, except one, below 135 mm. S.L. are immature; the exceptional fish (93 mm.) is a ripening female. The largest fishes (180–198 mm. S.L.) are females but there is one male of 179 mm. S.L.

Affinities. The colour pattern, small chest and nuchal scales and the sharply decurved head profile of *H. squamulatus* make at least large specimens readily identifiable. But, smaller individuals are less easily distinguished from specimens of *H. martini* (although the latter are adult at a size when most *H. squamulatus* are still immature). Unfortunately, little is known about the live coloration of sexually active male *H. squamulatus* but there are several similarities in the coloration of female *H. martini* and *H. squamulatus*, particularly in the striping and the yellowish coloration. In fishes of all sizes, *H. squamulatus* differ from *H. martini* in their less strongly decurved head profile, maxilla not extending so far posteriorly (never reaching a point below the pupil as is general in *H. martini*), in having a higher modal number of lateral line scales (35 *cf.* 33) and of scales between the pectoral and pelvic fin bases (9 *cf.* 7 or 8), and in the somewhat shallower body (23·5–35·1, M = 30·3% standard length, *cf.* 30·8–38·0, M = 34·4%).

When specimens over 100 mm. S.L. are compared, a number of additional morphometric differences are apparent: *H. squamulatus* has a longer snout, smaller eye and a longer lower jaw. Specimens less than 100 mm. S.L. have only one trenchant morphometric difference, the size of the eye (eye diameter in *H. squamulatus* is 25·9–30·4 [M = 28·3]% of head, *cf.* 29·4–37·5 [M = 31·7]% in *H. martini*).

Also resembling *H. squamulatus* (and *H. martini*, see Greenwood, 1962) is *Haplochromis michaeli*. The species differ in their preserved coloration (see above, and

Greenwood, *op. cit.*, p. 205), in the straighter, slightly concave, dorsal head profile of *H. michaeli*, and the greater posterior extension of the maxilla in that species (generally to below the pupil). Since specimens of *H. michaeli* over 100 mm. S.L. only are known, interspecific morphometric comparisons are restricted. These, however, show that *H. squamulatus* has a slightly shallower body (23·5–35·1, M = 30·3% of standard length, *cf.* 30·8–37·6, M = 34·3%), and a smaller eye (20·6–25·9, M = 23·3% head, *cf.* 24·0–29·1, M = 27·0% in *H. michaeli*). The nuchal scales of *H. squamulatus* are somewhat smaller (modal number of scales between the dorsal fin origin and the upper lateral line 8 or 9, *cf.* 6 or 7 in *H. michaeli*) as are those of the lateral line series (mode 35 *cf.* 33) ; the upper limit of the range for the lateral line scale count is also higher in *H. squamulatus* (38 *cf.* 35).

All in all, the resemblances between *H. squamulatus* and *H. martini* are greater than than those between *H. squamulatus* and H. *michaeli*, but the three species seem to form a closely related group within the more generalized piscivorous predators of Lake Victoria.

There is a certain similarity, albeit superficial, between *H. squamulatus* and *H. altigenis*. On closer examination, however, it does not seem likely that the resemblance can be construed as implying a close phyletic connection between the species. *Haplochromis altigenis* is probably a derivative of the *H. guiarti* stem.

In its general facies, *H. squamulatus* shows some similarity with *H. dichrourus*, but there is a very pronounced interspecific difference in coloration (*cf.* p. 90 with p. 67), as well as differences in some morphometric characters. *Haplochromis squamulatus* has a larger eye (20·6–25·9, M = 23·3% of head, *cf.* 19·4–22·6, M = 21·1) a shorter lower jaw (44·2–51·0, M = 47·5% of head, *cf.* 51·3–54·0, M = 52·7%) and a higher modal number of lateral line scales (35 *cf.* 33).

Phyletically, *H. squamulatus* and *H. michaeli* may represent slightly divergent developments (less so morphologically and ecologically in the former species) from an *H. martini*-like stem, an increase in adult size being a common factor in the two lines.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.262–272	Napoleon Gulf near Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.282–284	Fisherman's Point near Jinja .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.285–288	Beach near Nasu Point (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.289–295	Ramafuta Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.259–260	Off Buvuma Island (Buvuma Channel)	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.261	Grant Bay	E.A.F.R.O.
Genoa Museum C.E. 12977 (Holotype)	Jinja (Napoleon Gulf) . . .	Bayon
B.M. (N.H.) 1906.5.30.233–9	Nsonga	Degen
B.M. (N.H.) 1909.5.4.4–5	Sesse Islands	Bayon
B.M. (N.H.) 1966.3.9.278–281	Beach in Entebbe Harbour .	E.A.F.R.O.

B.M. (N.H.) 1966.3.9.258	Entebbe, Airport Beach . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.273–277	Kazima Island near Entebbe .	Uganda Fisheries Dept.
B.M. (N.H.) 1966.3.9.255	Old Bukakata Bay . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.257	Capri Bay, Mwanza . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.256	Mwanza Harbour . . .	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1901.6.24.86	Locality unknown . . .	Sir H. Johnston

Haplochromis barbarae sp. nov.

(Text-figs. 18 and 19)

HOLOTYPE: an adult female, 97 mm. standard length, from a beach near Nasu Point (Buvuma Channel); B.M. (N.H.) reg. no. 1966.2.21.5.

Named in honour of Mrs. Barbara Williams, whose drawings illustrate this and others of my papers.

DESCRIPTION: based on 9 specimens (including the holotype) 89·0–106·0 mm. standard length.

Depth of body 32·1–35·5 (M = 34·0) per cent of standard length, length of head 31·4–35·0 (M = 33·5) per cent. Dorsal head profile very slightly decurved or straight.

Preorbital depth 15·1–18·0 (M = 16·9) per cent of head length, least interorbital width 24·2–26·7 (M = 25·5) per cent. Snout as long as broad, its length 30·0–32·4 (M = 31·5) per cent of head, eye diameter 22·9–27·4 (M = 25·8), cheek depth 20·0–25·0 (M = 22·2) per cent.

Caudal peduncle 15·7–18·0 (M = 16·8) per cent of standard length, 1·4–1·7 times as long as deep (no well-defined mode).

Mouth very slightly oblique, the jaws equal anteriorly; lower jaw 36·6–41·2 (M = 38·0) per cent of head, 1·5–1·7 (in one fish 2·0) times as long as broad. Posterior tip of the maxilla reaching a point near the vertical through the anterior orbital margin.

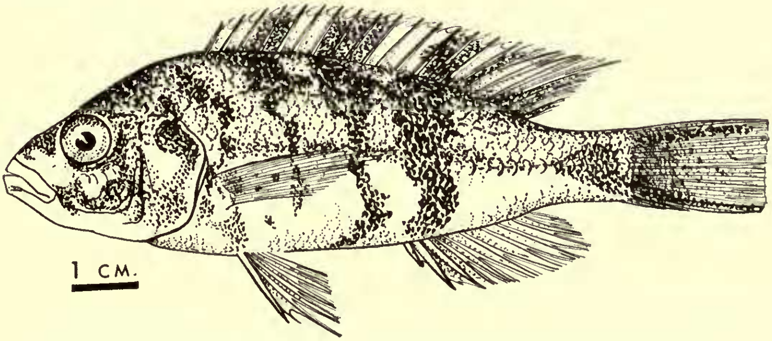

FIG. 18. *Haplochromis barbarae*. Drawn by Barbara Williams.

Gill rakers : of variable form, from moderately short and stout to slender and relatively elongate, but of constant form (except for the reduced lower rakers) in any one individual ; 8 or 9 rakers on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 33 (f.3), 34 (f.2) or 35 (f.4), cheek with 3 or 4 (rarely 2) rows. Seven (rarely 6½ or 8) scales between the upper lateral line and the dorsal fin origin, 7 or 8 (rarely 6 or 9) between the pectoral and pelvic fin bases. Scales on the ventral aspects of the chest are noticeably smaller than those situated laterally.

Fins. Dorsal with 25 (f.7) or 26 (f.2) rays, comprising 16 spinous and 9 (f.7) or 10 (f.2) branched rays. Anal with 11 (f.2), 12 (f.6) or 13 (f.1) rays, comprising 3 spines and 8 (f.2), 9 (f.6) or 10 (f.1) branched elements. Pectoral 25·0–29·2 (M = 26·7) per cent of standard length. Caudal truncate, scaled on its proximal half.

Teeth. In the outer row of both jaws, the teeth are relatively stout, bicuspid and slightly curved ; in a few specimens some posterolateral upper teeth are unicuspid and enlarged. There are 40–65 (M = 50) teeth in the outer row of the upper jaw.

Teeth forming the inner rows are relatively large and tricuspid, and are implanted somewhat obliquely so that the crowns point inwards. There are 2 or 3 inner rows in the upper jaw, and 2 (3 in one specimen) in the lower.

Osteology. No complete skeleton is available. The lower pharyngeal bone is, compared with that of similar species, small. Its dentigerous surface is broader than long, and narrows rapidly at about the midpoint so that not only is the whole bone relatively small, but so is the area of pharyngeal teeth. The teeth are fine, compressed and distinctly cuspidate ; they are rather sparsely distributed in from 22–24 rows.

Vertebral counts in 9 specimens are : 13 + 17 (f.8) and 13 + 18 (f.1) giving totals of 30 and 31.

Coloration : Live colours are unknown. *Preserved colours : Males* (*adult but quiescent*). Ground colour dark yellowish-brown. A well-defined lachrymal stripe is present, as are faint traces of two transverse, parallel stripes across the snout. There is some darkening over the preoperculum but this is not concentrated into a

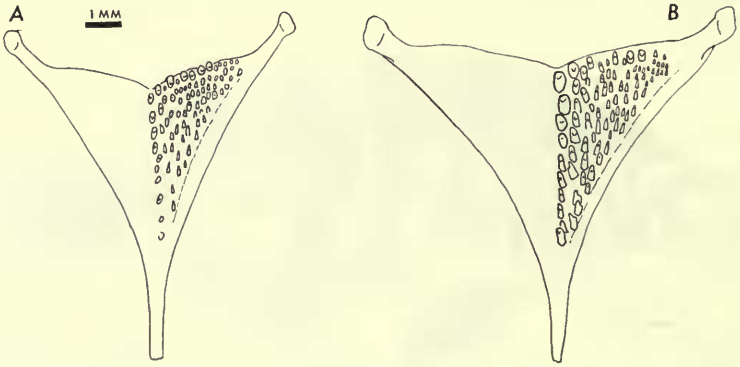

FIG. 19. Lower pharyngeal bones (in occlusal view, with dentition shown on one side only) of (A) *H. barbarae*, and (B) *H. chromogynos*.

bar or stripe. The branchiostegal membrane is dark, most intensely so below the opercular bones. On the flank is a faint midlateral stripe, and four even fainter and incomplete vertical bars. Dorsal and anal fins are yellowish with a sooty overlay, the anal being darkest along its proximal third; anal ocelli very faint. Pelvics sooty over a yellowish ground. Caudal yellowish on the margins and distal third, dark brown proximally.

Females (*adult.*) Three distinct colour patterns occur; two of these are probably identical with the polychrome patterns described for live *Hoplotilapia retrodens* (see Greenwood, 1956).

The colour pattern corresponding with the modal coloration in other polychromatic species has a yellow-brown ground colour with a distinct midlateral dark stripe running from the opercular margin to the caudal origin, and extending onto the caudal fin itself for about half its length; in two specimens there are four, narrow vertical bars on the flanks, extending from the dorsal fin base almost to the ventral outline. In all specimens a very faint upper line is situated slightly above the upper lateral line. All fins are yellowish-brown. Three out of the eight female specimens have this type of coloration.

The second pattern is a piebald, black on silvery-yellow (to yellow brown), the black pigment arranged in blotch-like bars of variable width and dorso-ventral extent. Some blotches extend onto the dorsal, caudal, anal and pelvic fins. The cheeks and snout may be blotched or clear. All fins are yellowish. This pattern does not differ from that shown by other species with a piebald coloration in females. Four of the eight *H. barbarae* females are piebald.

The third pattern, found only in one specimen, has an orange-yellow background peppered with fine melanophores which are, in places, aggregated into blotches (especially on the dorsum) with an irregular distribution. Some dark blotches occur on all fins (but especially the dorsal and caudal); these spots are smaller than those on the body. The ground colour of all fins is light orange-yellow.

Ecology. Habitat. The nine known specimens came from three different sites. Two of these are shallow, exposed and sandy beaches, the third, shallow water (*ca.* 10 ft. deep) over a hard substrate a short distance off-shore and near the water-lily zone fringing a papyrus swamp.

Food. Seven of the 9 specimens examined contained ingested matter in the guts. In each case this consisted of from 1–8 (mode 5) recently fertilized cichlid ova. In two specimens these could have been part of the fish's own brood swallowed during capture, because the fishes have recently spent ovaries. But, judging from the advanced stages of oogenesis shown by four other specimens, and the fact that the fifth is a male, it seems reasonable to conclude that the embryos were taken as food (see Greenwood, 1959, for a discussion of other paedophagous *Haplochromis* species).

Breeding. Nothing is known about the breeding habits of *H. barbarae*. All nine specimens are sexually mature; the sole male (102 mm. S.L.) is the second largest specimen.

Affinities. Anatomically, *H. barbarae* is very like *H. brownae*, a generalized species exhibiting many characters suggestive of affinity with anatomically generalized predators such as *H. guiarti* (Greenwood, 1962).

Haplochromis barbarae differs from *H. brownae* in having a narrower interorbital (24·2–26·7, M = 25·5% of head, *cf.* 26·0–34·0, M = 29·8%), a smaller eye (22·9–27·4, M = 25·8% of head, *cf.* 26·0–31·3, M = 28·6%), fewer gill rakers (8 or 9, *cf.* 9–12 [modes 10 and 11]), and smaller scales, especially on the ventral aspects of the chest. There is also a difference in dention in that the outer teeth of this species are stout bicuspids whereas in *H. brownae* of a similar size the teeth are slender unicuspids.

It differs from *H. guiarti* in having a shorter snout (30·0–32·4, M = 31·5% of head, *cf.* 31·7–37·5, M = 34·4) and lower jaw (36·6–41·2, M = 38·0% of head, *cf.* 39·2–48·2, M = 44·4%), fewer gill rakers (8 or 9, *cf.* 9–11, mode 10) and, at comparable sizes, the presence of bicuspid teeth anteriorly in both jaws (unicuspid in *H. guiarti*).

Because of its generalized anatomy and unspecialized dentition, *H. barbarae* closely resembles a number of other species in the Lake Victoria flock, *viz. H. cinereus, H. macrops, H. lacrimosus* and *H. chromogynos* (see Greenwood, 1959 for the latter species and Greenwood, 1960 for the three former). In addition to their anatomical similarities, *H. barbarae* and *H. chromogynos* also share (with several other and structurally unrelated species) the piebald coloration in females. However, *H. barbarae* differs from *H. chromogynos* in having a longer lower jaw (36·6–41·2, M = 38·0% of head, *cf.* 30·0–34·4, M = 32·5%), and, when specimens of equal size are compared, bicuspid instead of slender unicuspid teeth (specimens of *H. chromogynos* < 95 mm. S.L. have a mixed bi- and unicuspid dentition but larger individuals have only unicuspid teeth). The shape of the pharyngeal bone differs in the two species, and it is this character (see p. 94 and fig. 19) which most readily distinguishes *H. barbarae* from the other three species mentioned above, none of which is known to have piebald females or paedophagous habits.

The peculiar feeding habits of *H. barbarae* immediately suggest some affinity with the other paedophagous *Haplochromis* species, and because *H. barbarae* is anatomically unspecialized, particularly with the more " generalized " paedophages, *H. obesus* and *H. cronus*. However, in many morphological details these two differ considerably from *H. barbarae*. For instance, the peculiar dental morphology of *H. obesus* (with the small teeth deeply embedded in the gums), and the stout unicuspid teeth of *H. cronus*, serve as immediately diagnostic characters, as do the several morphometric differences between the species. It is of interest, however, to recall that piebald females occur in all three species ; but, since this character appears in other and widely different species, it is not thought to have any phyletic significance.

Any supposed close phyletic relationship between *H. barbarae* and the other members of the paedophagous species group would also be difficult to substantiate. At present all that can be suggested is that *H. barbarae* might represent an isolated line, derived from a generalized and probably insectivorous stem, paralleling trophically the paedophagous species group (itself probably of diphyletic origin). Alternatively, *H. barbarae* might represent a survivor of the stem from which such species as *H. cryptodon* and *H. microdon* arose ; more will have to be learned about the anatomy of *H. barbarae* before this possibility can be substantiated.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.3.9.243	Napoleon Gulf, off Jinja . .	E.A.F.R.O.
B.M. (N.H.) 1966.2.21.5 (Holotype)	Beach near Nasu Point (Buvuma Channel) . . .	E.A.F.R.O.
	TANZANIA	
B.M. (N.H.) 1966.3.9.244–251	Beach near Majita . . .	E.A.F.R.O.

Haplochromis tridens Regan and Trewavas, 1928

(Text-fig. 20)

Haplochromis tridens Regan & Trewavas, 1928, *Ann. Mag. nat. Hist.* (10), **2**, 226.

LECTOTYPE : a fish 116·0 mm. standard length (caudal fin damaged), B.M. (N.H.) reg. no. 1928.6.2.41, collected in Tanzanian waters at Michael Graham's station 234 (1° 4′ S, 32° 13′ E), at a depth of over 100 ft. (Graham, 1929).

DESCRIPTION : based on 16 specimens (including the lectotype and the paralectotype) 72–119 mm. standard length.

Depth of body 30·1–36·2 (M = 33·5) per cent of standard length, length of head 32·0–37·2 (M = 35·4) per cent. Dorsal head profile straight, but interrupted by the prominent premaxillary pedicels, sloping steeply at 40°–45°. The cephalic lateral line system with prominent pores, especially those of the preopercular and preorbital canals. These pores are probably larger than in any Lake Victoria *Haplochromis* (including *H. pachycephalus* and *H. boops*).

Preorbital depth 16·0–20·9 (M = 17·2) per cent of head, least interorbital width 15·0–19·5 (M = 16·7) per cent. Snout 1·0–1·3 (mode 1·1) times as long as broad, its length 28·0–34·8 (M = 30·4) per cent of head. Eye with an oval, horizontally aligned pupil, eye diameter 25·6–34·0 (M = 30·7) per cent of head, depth of cheek 17·5–22·8 (M = 19·2) per cent.

Caudal peduncle 16·7–19·8 (M = 17·9) per cent of standard length, 1·4–1·9 (mode 1·6) times as long as deep.

Mouth horizontal or slightly oblique, lower jaw projecting slightly and with a distinct mental projection ; length of lower jaw 43·3–51·8 (M = 47·5) per cent of head, 2·0–2·8 (mode) times as long as broad. Premaxilla slightly expanded in the midline. Posterior tip of the maxilla generally reaching to below the anterior part of the eye, and occasionally to below the pupil ; rarely reaching only to the vertical through the anterior margin of the orbit.

Gill rakers : relatively slender, except for the lower 1–3 which are reduced, and the upper 2–4 which are usually flat ; 8–11 (mode 9) on the lower part of the first gill arch.

Scales : strongly ctenoid, especially those on the chest region. Lateral line with 31 (f.4), 32 (f.5), 33 (f.4) or 34 (f.2) scales. Cheek with 3 (mode) or 4 rows. Five and a half to 6½ (modes 6 and 6½) scales between the upper lateral line and the dorsal fin origin, 5–6½ (mode) between the pectoral and pelvic fin bases.

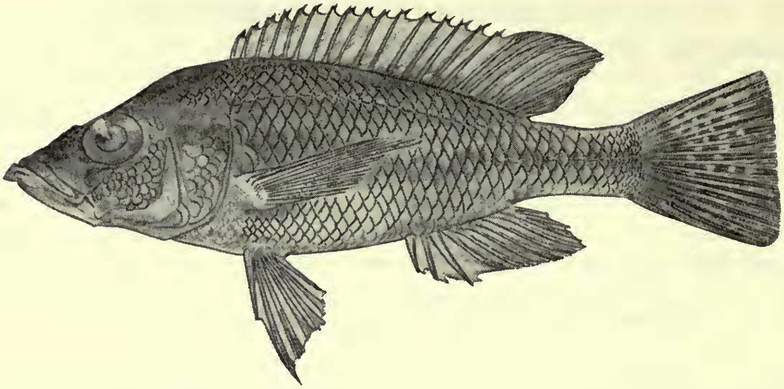

FIG. 20. *Haplochromis tridens*, paralectotype, about ·73 times natural size. Drawn by Miss M. Fasken.

Fins. Dorsal with 23 (f.7), 24 (f.7) or 25 (f.2) rays, comprising 15 (f.4) or 16 (f.12) spinous, and 7 (f.6), 8 (f.6), 9 (f.3) or 10 (f.1) branched rays. Anal with 10 (f.10), 11 (f.5) or 12 (f.1) rays, comprising 3 spines and 7 (f.10), 8 (f.5) or 9 (f.1) branched elements. (*N.B.* More than usual difficulty was experienced in deciding if the last dorsal and anal ray was a single, deeply divided element, or two distinct rays ; this may account for the number of specimens with low (7) branched ray counts). Pectoral 27·0–33·3 (M = 29·3) per cent of standard length. Pelvics with the first branched ray produced, proportionately more so in adult males. Caudal truncate.

Teeth. The trivial name "*tridens*" was given to the species because the larger of the two syntypes had only tricuspid teeth in the outer tooth row of both jaws, an unusual (probably unique) feature for a *Haplochromis* species. This condition is, however, rare in the species. Uni-, bi- and tricuspid outer teeth may all occur in a single specimen. Tricuspid teeth, at least in the upper jaw, are usually found posterolaterally, the bi- and unicuspids laterally and anteriorly. This arrangement is by no means constant ; in some specimens tricuspids occur anteriorly and anterolaterally. One fish (72 mm. S.L.) has only bicuspids in the upper jaw, and another (81 mm.) only unicuspids. There is no apparent correlation between the predominance of any one tooth form and the size of the fish. In three out of the sixteen specimens examined, no tricuspid outer teeth were found in either jaw.

There are 58–80 (M = 66) teeth in the outer row of the upper jaw.

Variation in the type of outer teeth occurring in the lower jaw follows the same pattern as in the upper jaw.

Teeth forming the inner rows in both jaws are predominantly tricuspids. These teeth are relatively large, are stout, and have the median cusp larger than the lateral ones. There are usually 2 inner rows (occasionally 3, rarely 4) in the upper jaw, and 2 (rarely 1) in the lower.

Osteology. No entire skeleton is available. The lower pharyngeal bone has its dentigerous surface equilateral or slightly broader than long. The lower pharyngeal teeth have cuspidate, compressed crowns, and cylindrical necks ; the teeth are arranged in 22–26 rows.

Vertebral counts in 10 specimens are: 13 + 16 (f.7) and 13 + 17 (f.3), giving totals of 29 and 30.

Coloration. Live colours are unknown. *Preserved specimens : Males* (*adult and sexually active*) *:* ground colour grey-blue (gun-metal) above the upper lateral line, greyish silver on the flanks, and light dusky silver on the chest and belly. Dorsal and caudal fins hyaline. Anal hyaline except for a dusky area between the spines, and black lappets ; the dusky area extends as a fairly distinct line at the base of the spinous part, and may be expanded basally onto the soft fin. There are two, large, grey-white anal ocelli. Pelvics dusky, darkest on the lateral four-fifths of the fin.

Males (adult but quiescent) have a ground coloration more like that of females. All fins are hyaline except for a faint darkening between the anal spines, and on the pelvic fins.

Females (*juvenile and adult*) *:* greyish silver above, shading to silver below. One specimen (ovaries ripening) is darker dorsally (almost brown), and has a broad, interrupted midlateral stripe running from behind the operculum to about half the length of the caudal fin (on which the stripe narrows) ; the band is interrupted at about the middle of its length. All fins yellowish to hyaline.

Ecology. Habitat. Excepting the two types, all the material came from one trawl haul at an unknown locality (thought to be off the Kenya coast). The types came from deep water (more than 100 ft.) some distance off-shore, and from over a soft bottom. The large eyes and hypertrophied pores of the cephalic lateral line system certainly suggest adaptations to a deepwater habitat.

Food. Only 6 of the 10 specimens examined (all from the same, and unknown, locality) contained ingested material in the gut. In each, the predominant contents are undigested blue-green algae, and empty diatom frustules. Two specimens have, in addition, a few fragments of Crustacea, and some unidentifiable insect remains.

Breeding. All fourteen of the non-typical specimens are adults. The types are not well-preserved internally, but both appear to be females.

Affinities. The admixture of tri-, uni- and bicuspid outer teeth together with the hypertrophy of the cephalic lateral line pores, provide a trenchant means of distinguishing *H. tridens* from other species in the lake. Indeed, it is difficult to suggest any close relationship between this species and any other so far considered. Perhaps some relationship will become apparent when more is known about the numerous and small species of *Haplochromis* which make up the bulk of fishes caught by trawling in the deeper waters of Lake Victoria (Greenwood, unpublished). Anticipating these results, it is possible to say that the elongate body and general " predatory " facies (especially the large mouth) of *H. tridens* are not common amongst these species, and nor is the *H. tridens* dental type.

Amongst the larger species with a predatory facies, *H. tridens* most closely resembles *H. victorianus*. There are, however, many differences between the species, not least of which are their differences in ecology and the much smaller adult size of *H. tridens*. *Haplochromis victorianus* differs also in its dentition, broader interorbital region (21·5–24·5, M = 22·6% of head, *cf.* 15·0–19·5, M = 16·7%) smaller and rounder eye (21·7–25·5, M = 23·6% head, *cf.* 25·6–34·0, M = 30·7%), and deeper cheek (22·5–26·2, M = 24·6% head, *cf.* 17·5–22·8, M = 19·9%). It should be remembered, however, that the data for *H. victorianus* are derived from larger specimens than are available for *H. tridens*, and that the most trenchant morphometric differences are in characters most affected by allometric growth. Nevertheless, it seems very unlikely that *H. victorianus* and *H. tridens* are close relatives.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	TANZANIA	
B.M. (N.H.) 1928.6.2.41 (Lectotype)	104′ S, 32° 13′ E	M. Graham
B.M. (N.H.) 1928.6.2.42 (Paralectotype)	104′ S, 32° 13′ E	M. Graham
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.152–165	Locality unknown (? Kenya coast)	E.A.F.R.O.

Haplochromis orthostoma Regan, 1922

(Text-fig. 21)

Pelmatochromis spekii (part): Boulenger, 1915, *Cat. Afr. Fish.*, **3**, 417.
Haplochromis orthostoma Regan, 1922, *Proc. zool. Soc. Londn.*, 184, fig. 9.

HOLOTYPE: a male (probably adult), 91 mm. standard length (B.M. [N.H.] reg. no. 1912.10.15.67) from Lake Salisbury (Kyoga system). The specimen is now in very poor condition, and has lost most of its scales.

This species, possibly one of the two most distinctive looking members of the Victoria-Kyoga flock, was described from a single specimen. Since then, two further specimens have been collected from Lake Salisbury, and three superficially similar specimens have been caught in Lake Victoria. The latter specimens differ from the Salisbury fishes in their dentition (and some other characters) and are thought to represent a distinct species. It is for this reason that I am redescribing the Lake Salisbury species in this paper.

The unusual physiognomy of *H. orthostoma* is well shown in text-figure 21; the snout and nuchal region meet at a distinct angle, the nuchal musculature not bulging anteriorly and laterally. Since there are only three specimens available, morphometric characters are tabulated below. The holotype is indicated with an asterisk.

S.L. (mm.)	Depth †	Head †	Preorb. %	Interorb. %	Snout %	Eye %	Cheek %	Caudal Peduncle†
67·5	37·0	36·0	19·6	20·4	32·7	24·5	24·5	19·3
83·0	35·0	36·1	20·0	23·3	30·0	21·7	30·0	17·5
*91·0	36·3	35·5	18·5	21·5	30·8	22·8	30·8	16·5

† Per cent of standard length.
% Per cent of head length.

Mouth very oblique, sloping at *ca* 50°–70°, the lower jaw projecting, its length 51·0–56·6 per cent of head length, and 2·5–3·4 times as long as broad. Lips not thickened, the lower jaw with a distinct mental protuberance. Posterior tip of the maxilla reaching a point about midway between the vertical through the anterior orbital margin and that through the nostril. Snout 1·1–1·3 times as long as broad, its dorsal surface slightly rounded, the premaxillary pedicels not prominent.

Caudal peduncle 1·5–1·6 times as long as deep.

Gill rakers : moderately stout, the lower 1–3 reduced, the upper 2 or 3 flattened (anvil-shaped in one fish) ; 9 or 10 on the lower part of the first gill arch (11 on one arch of a fish with 9 rakers on the other arch).

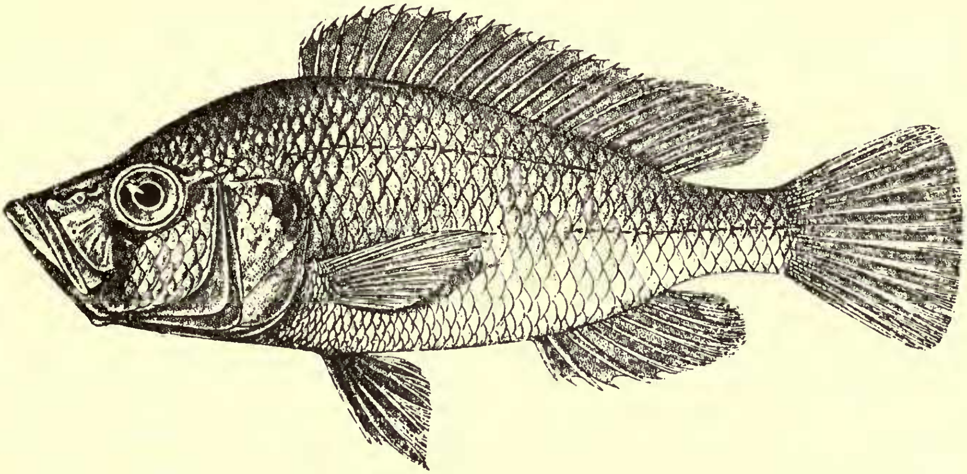

FIG. 21. *Haplochromis orthostoma*, holotype. From Regan, *Proc. zool. Soc.*, about ·86 times natural size.

Scales : ctenoid ; lateral line with 30 or 31 scales (Regan gives 33 for the now scaleless type), cheek with 3 or 4 rows (4 or 5 in the type according to Regan). Six or 6½ between the upper lateral line and the dorsal fin origin (6 or 7 in the type acc. Regan), 6 or 7 between the pectoral and pelvic fin bases, the chest scales small.

Fins. Dorsal with 14 (f.1) or 15 (f.2) spines and 9 branched rays, anal with 3 spines and 8 (f.2) or 9 branched rays. First branched pelvic ray not produced in the type, but elongate in the two other specimens (male and female). Caudal subtrucate.

Teeth. In the two larger specimens (83 and 91 mm. S.L.), the outer teeth in both jaws are a most distinctive feature. These teeth are slender and unicuspid with sharply curved tips directed medially ; those situated anteriorly are somewhat larger than the others. There are 66 and 61 teeth in this row for the two specimens respectively. In the lower jaw, the outer teeth, at least anteriorly, are somewhat stouter than their opposites in the upper jaw.

The smallest specimen (67·5 mm. S.L.) has outer teeth quite unlike those of the larger individuals. In the upper jaw, the anterior and lateral teeth are stout and bicuspid, those situated laterally and posteriorly are stout and tricuspid. All outer teeth in the lower jaw are bicuspid and stout, and are a little stouter than the upper jaw teeth. There are 68 teeth in the outer row of the upper jaw.

The inner teeth in the two larger fishes are unicuspid, small, slender and implanted obliquely ; in the smallest fish they are small and tricuspid.

The dental arcade in all specimens is V shaped with a rounded apex ; there are 2 inner tooth rows in the upper jaw, and 1 or 2 rows in the lower jaw.

Osteology. No complete skeleton is available. The lower pharyngeal bone has a triangular and equilateral dentigerous area. The teeth are relatively slender, with bicuspid and weakly compressed crowns, and are arranged in 20–22 rows ; except in the smallest fish the teeth of the two median rows are coarser than the lateral rows.

Vertebral counts for 2 specimens are : 13 + 16 (type) and 12 + 16.

Coloration : Live colours are unknown. The type is now completely colourless ; originally it was described as greyish, with a dark lachrymal stripe, and blackish pelvic fins. A juvenile female has a brown ground coloration, with very faint traces of four broad vertical bars on the flanks running from the dorsal fin origin to about the level of the ventral margin of the pectoral fin. No lachrymal stripe is visible. The lower jaw (especially over its anterior half) is rather dusky. The dorsal and caudal fins are yellowish, the former with black lappets. Anal dusky yellow. Pelvics faintly dusky, especially at their tips. Pectorals yellowish-grey.

Adult Male (*probably fixed in alcohol*) *:* light brown above, shading to silver on the mid-flanks, and silvery white on the belly. Snout dark, as are the lips ; branchiostegal membrane pale. A faint lachrymal stripe is visible. Dorsal fin greyish, with black lappets. Anal greyish, with two white ocelli. Caudal grey, the melanophores most concentrated along its midline. Pelvics dark along the anterior quarter, hyaline elsewhere.

Ecology. No information is available on the habitat or food of *H. orthostoma*, nor is there any information on the breeding habits of the species. The two males (91 and 83 mm. S.L.) are adult, and the female (67·5 mm.) is apparently immature.

Affinities. The peculiar head shape, large and very oblique mouth, coupled with the peculiar tooth form (at least in the larger fishes), serve to distinguish the species from all others in the Lake Victoria-Kyoga flock. The nearest relative is *H. parorthostoma* from Lake Victoria (see below). Further material, and field observations, may yet show that the two species are not distinct at that level.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
B.M. (N.H.) 1912.10.15.67 (Holotype)	Lake Salisbury	Presented by F. J. Jackson
B.M. (N.H.) 1958.12.5.173	Ongino, Lake Salisbury . .	Pitman
B.M. (N.H.) 1966.3.9.252	Lake Salisbury	E.A.F.R.O.

Haplochromis parorthostoma sp. nov.

(Text-fig. 22)

HOLOTYPE: an adult male, 117 mm. standard length, from near Zero Island (Buvuma Channel), Uganda. B.M. (N.H.) reg. no. 1966.2.21.4.

DESCRIPTION. The overall similarity between this species and *H. orthostoma* is great, particularly since both share a peculiar head profile not seen in any other *Haplochromis* species from Lakes Victoria or Kyoga.

The dorsal head profile is strongly concave, with the nuchal region meeting the snout at a noticeable but rounded angle, the junction emphasized by an anterior bulge of the cephalic epaxial body musculature. This muscular protuberance gives the fish a pronounced " forehead ", especially in the frontal plane.

Since only three specimens are available, morphometric data are tabulated below; the holotype is marked with an asterisk.

S.L. (mm.)	Depth †	Head †	Preorb. %	Interorb. %	Snout %	Eye %	Cheek %	Caudal Peduncle†
86·0	38·4	35·0	16·7	20·0	31·6	27·7	25·0	17·5
110·0	42·3	36·4	17·5	17·5	33·8	25·0	27·5	12·7
*117·0	41·0	35·0	19·5	19·5	34·9	24·4	26·8	14·5

† Per cent of standard length.
% Per cent of head length.

Mouth oblique, sloping upwards at *ca.* 40°–50°, jaws equal anteriorly, or the lower projecting slightly. Lower jaw length 48·3–53·5 per cent of head, 2·3–2·4 times as long as broad; chin with a distinct protuberance. Posterior tip of the maxilla reaching a point nearer the vertical through the anterior orbital margin than one through the nostril. Snout 1·2 times as long as broad, with a convex dorsal surface; premaxillary pedicels not prominent. Lips moderately thickened.

Caudal peduncle 1·1–1·3 times as long as deep.

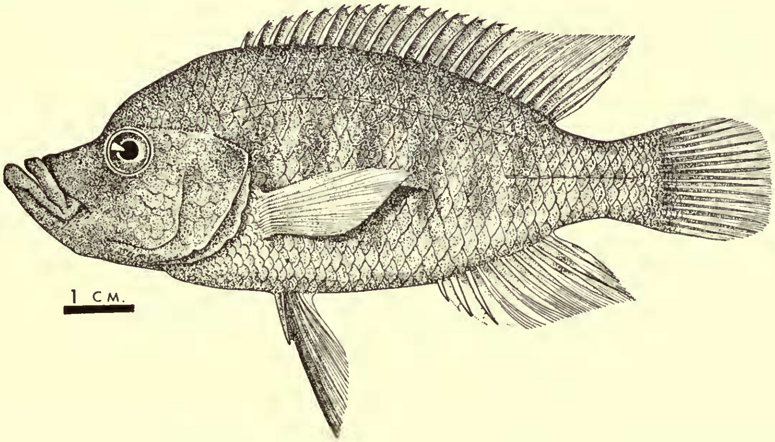

FIG. 22. *Haplochromis parorthostoma.* Drawn by Lavinia Beard.

Gill rakers : moderately stout (relatively stouter in one specimen), the lower 1–3 reduced, the upper 2 or 3 expanded and anvil-shaped ; 9 (f.2) or 10 rakers on the lower part of the first gill arch.

Scales : ctenoid, lateral line with 30 or 32 (f.2) scales, cheek with 2 or 3 rows (in the former specimen, the scales not covering the ventral aspects of the cheek). Six or 7 scales between the upper lateral line and the dorsal fin origin, 6 or 7 between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.2) or 16 spines and 8, 9 or 10 branched rays. Anal with 3 spines and 8 or 9 (f.2) branched rays, the spines short and stout. Pectoral 24·5–26·2 per cent of standard length. First branched pelvic ray not or slightly produced (all specimens are males). Caudal almost rounded, scaled on its basal two-thirds.

Teeth. The outer row in both jaws is composed of unicuspid, slender and slightly curved teeth, the curvature being gentle and not confined to the distal part of the tooth (*cf. H. orthostoma*, p. 101) ; in one fish, the last three teeth in the upper jaw are larger, stouter and straighter than the anterior ones. A few bicuspid, moderately stout teeth occur posteriorly in the lower jaw of the smallest (86 mm.) fish. In no specimen are the lower jaw teeth stouter than those in the upper jaw. There are 38, 40 and 52 teeth in the outer row of the upper jaw.

Teeth forming the inner series are small, tricuspid and weakly tricuspid, and are arranged in 3 or 4 rows in the upper jaws and in 2 rows in the lower.

The dental arcade is V shaped, with the apex broadly rounded.

Osteology. No complete skeleton is available. The lower pharyngeal bone has its triangular dentigerous surface as long as broad, or slightly broader than long. The teeth, arranged in 24–30 rows, are fine, with weakly compressed bicuspid crowns ; those in the two median rows are but slightly larger than the lateral teeth.

Vertebral counts in 3 specimens are : 13 + 15 and 13 + 16 (f.2).

Coloration : Live colours are known for a sexually active (but not ripe) *male.* Ground colour dark slate-grey, with faint vertical bars of a darker shade. Dorsal fin dark grey with crimson lappets on the posterior two-thirds of the spinous part, and a dark crimson margin to the entire soft part. Caudal dark grey with a crimson flush, particularly intense on its lower half. Entire anal fin, except for a dark base, crimson. Pelvics black on the anterior third, remainder dull crimson.

Preserved material : Males (adult). Ground colour light brown (including the branchiostegal membrane in two fishes ; this membrane blackish in the third specimen) ; flank crossed by 5 or 6 dark but incomplete bars, each bar originating just above the upper lateral line and extending to about the level of the ventral margin of the pectoral fin. A fairly distinct vertical lachrymal stripe runs from the anteroventral margin of the orbit to the angle of the lower jaw. Dorsal fin yellowish-brown along its margin, but dark brown between the rays. Anal yellowish, sooty or dark brown between the branched rays ; very faint indications of 2 or 3 whiteish ocelli. Caudal light to dark brown (almost black). Pelvics dusky on the anterior third to half, otherwise hyaline.

Ecology. One specimen came from an exposed, sandy beach, another from a rocky outcrop in about 20 ft. of water near an off-shore island, and the third from over a rocky shelf in about 40 ft. of water, also near an island.

No information is available on the food of *H. parorthostoma*. The three specimens are adult males.

Affinities. *Haplochromis parorthostoma* seems to be very closely related to *H. orthostoma* of the Kyoga system, at least in its peculiar head-shape. There is, however, a marked interspecific difference in the shape of the outer teeth. In *H. parorthostoma* these teeth are gently curved, whereas in *H. orthostoma* they have sharply recurved crowns but relatively straight necks. Furthermore, the inner teeth of *H. orthostoma* are unicuspid and arranged in one or two rows, but in *H. parorthostoma* are tricuspid and arranged in three or four rows in the upper jaw (two rows in the lower). An exception (at least with regard to outer tooth shape) is provided by the smallest specimen of *H. orthostoma* whose stout, erect and bicuspid teeth do not resemble those of its larger congeners (or, for that matter, *H. parorthostoma*). But, since the cranial morphology of this small fish is so like that of larger *H. orthostoma* individuals it is included in that species.

Haplochromis parorthostoma and *H. orthostoma* differ in characters other than dental ones. The bulging cranial epaxial muscles of *H. parorthostoma* impart a different shape to the dorsal head profile, which is further modified by the less oblique mouth. The available samples also suggest that *H. parorthostoma* has a bigger eye than *H. orthostoma* (and this despite the fact that the specimens of *H. parorthostoma* are larger) and probably a shorter and broader lower jaw.

Clearly, much more material is required before it will be possible to reach more definite conclusion about the status of the two species. Even then the decision will be complicated by the fact that they are allopatric, and their areas of distribution are physically isolated (now by the virtually impenetrable Owen Falls dam, and previously by the Ripon Falls, perhaps not a complete barrier to migration from Lake Victoria to the Kyoga system).

For the moment it is not possible to speculate on the wider relationship of these two species.

STUDY MATERIAL AND DISTRIBUTION RECORDS

Museum and Reg. No.	Locality	Collector
	Uganda	
B.M. (N.H.) 1966.2.21 (Holotype)	Near Zero Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.253	Near Zero Island (Buvuma Channel) . . .	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.254	Near Kazima Island . . .	Uganda Fish. Dept.

Haplochromis apogonoides sp. nov.

(Text-fig. 23)

HOLOTYPE an adult male, 118 mm. standard length, from Ekunu Bay, Uganda. B.M. (N.H.) reg. no. 1966.2.21.3.

Named " *apogonoides* " because of its fancied resemblance to the genus *Apogon*.

Description: based on eight specimens (including the holotype) 112–132 mm. standard length; with one exception (a quiescent female) all are males.

Depth of body 36·0–39·6 (M = 38·1) per cent of standard length, length of head 35·0–37·2 (M = 36·1) per cent. Dorsal head profile curved (strongly so in some specimens), sloping fairly steeply (*ca.* 40°), the premaxillary pedicels not prominent.

Preorbital depth 13·6–16·7 (M = 15·2) per cent of head length, least interorbital width 27·5–31·0 (M = 29·5) per cent. Snout 1·3–1·5 (mode 1·4) times as broad as long, its length 29·3–33·4 (M = 31·2) per cent of head, eye 25·3–27·5 (M = 26·6), depth of cheek 27·8–31·0 (M = 29·3) per cent.

Caudal peduncle 15·3–19·8 (M = 18·0) per cent of standard length, 1·5–1·7 times as long as deep.

Mouth slightly to moderately oblique, lips somewhat thickened, the jaws equal anteriorly. Lower jaw 45·0–51·0 (M = 47·9) per cent of head, 1·2–1·5 (modal range 1·4–1·5) times as long as broad. Posterior tip of the maxilla reaching to below the pupil. Premaxilla not expanded medially.

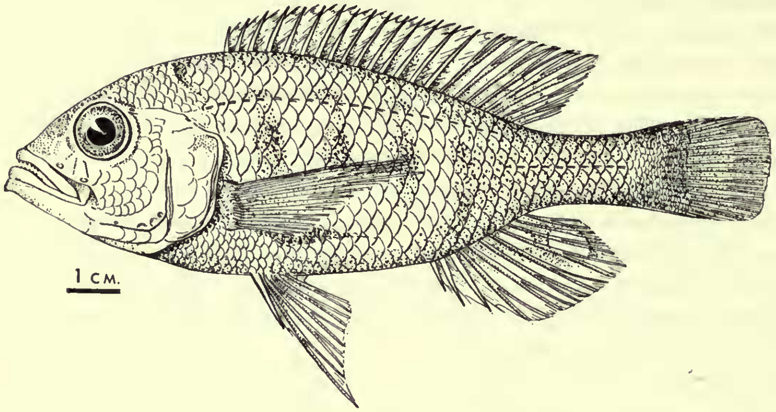

Fig. 23. *Haplochromis apogonoides.* Drawn by Barbara Williams.

Gill rakers: stout, the lower 1–3 reduced, the upper 3 or 4 flat; 8–10 on the lower part of the first gill arch.

Scales: ctenoid; lateral line with 32 (f.4), 33 (f.3) or 34 (f.1) scales. Cheek with 3 or 4 (mode) rows. Six to 8 (mode 6) scales between the upper lateral line and the dorsal fin origin, 6–8 (modes 6 and 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 22 (f.1), 24 (f.6), or 25 (f.1) rays, comprising 14 (f.2) or 15 (f.6) spinous and 8 (f.1), 9 (f.5) or 10 (f.2) branched rays. Anal with 10 (f.1), 11 (f.5) or 12 (f.2) rays, comprising 3 spines and 7 (f.1), 8 (f.5) or 9 (f.2) branched elements. Pectoral 29·0–34·1 (M = 30·8) per cent of standard length. Pelvics with the first ray slightly produced. Caudal truncate to subtruncate, scaled on its basal half to two-thirds.

Teeth. The outer teeth in both jaws are a characteristic feature of the species, being unicuspid, moderately stout and with very strongly recurved tips. Such teeth are otherwise found only in the *H. sauvagei* species group (see Greenwood, 1957). There are 50–60 (M = 58) teeth in the outer row of the upper jaw.

The inner teeth are also unicuspid, large and recurved, and are implanted obliquely. There are 2 rows in the upper jaw, and 1 or 2 rows in the lower jaw. A distinct space separates the inner series from the outer row.

Osteology. No complete skeleton is available. The lower pharyngeal bone is relatively stout, the dentigerous surface noticeably broader than long ($1\frac{1}{5}$ to $1\frac{1}{4}$ times). The teeth are stout and cuspidate, and are arranged in from 16–20 rows, those of the two median rows being slightly coarser than the others.

Vertebral counts in 7 specimens are : 13 + 15 (f.1), 13 + 16 (f.5) and 14 + 16 (f.1), giving totals of 28–30.

Coloration. Live colours are unknown. *Preserved coloration : Males* (*adult and sexually active, but probably not ripe*). Ground colour light yellow-brown, with a silvery underlay on the flanks. Belly, chest and branchiostegal membrane dusky, the branchiostegal membrane darkest below the opercular region. On the flanks there are faint traces of 4 or 5 fairly broad vertical bars which become very faint dorsally and ventrally ; the anterior 3 or 4 bars merge ventrally with the dark belly coloration. A dark lachrymal stripe is present ; it does not reach the ventral margin of the preorbital, but appears to pass upwards across the eye. Dorsal fin yellowish, the soft part maculate in some specimens ; also in some fishes the lappets are black. Caudal yellowish marginally and on the distal third to quarter, dark yellow-brown proximally. Anal yellowish, with one large greyish to whiteish ocellus faintly outlined in black. Pelvics sooty, the colour less intense between the last two or three rays.

Female (*adult and quiescent*). Ground colour greyish-silver. A very faint lachrymal bar extends from below the orbit to below the posterior tip of the maxilla ; a dark spot on the upper part of the eye suggests that this bar may pass across the eye. All fins are yellowish, the dorsal with dusky lappets, and the pelvics with a faint duskiness over the anterior rays.

Ecology. *Habitat*. The species has been caught in two localities only. In one, a sheltered bay, the water was between 20 and 30 feet deep, and the substrate of organic mud. The second locality was at a depth of about 80 ft in the Buvuma Channel, near Buvuma Island ; again the substrate (on which the nets were set) was organic mud.

Food. Regrettably, the gut was empty in all except one specimen ; this fish contained only a little, unidentifiable sludge.

Breeding. Apart from the sexually inactive female (132 mm. S.L.), all the specimens are adult and active males.

Affinities. The stout, unicuspid outer teeth with sharply recurved crowns immediately suggest affinity with *H. sauvagei*, *H. prodromus* and *H. granti* (Greenwood, 1957). Like these species, the dorsal head profile of *H. apogonoides* is strongly rounded. However, unlike these species, there are fewer rows of inner teeth in *H. apogonoides*, there is a distinct interspace between the inner and outer tooth rows, and the lower jaw is much longer (45·0–51·0, M = 47·9% head *cf.* 30·6–37·7, M = 34·5% for *H. sauvagei*, 30·5–37·8, M = 34·3% for *H. prodromus*, and 22·2–30·6, M = 26·8% for *H. granti*). *Haplochromis apogonoides* also differs from these species in its broader snout, and from *H. granti* in the anatomy of the jaws (see Greenwood, 1957).

Superficially, *H. apogonoides* resembles *H. cronus* (Greenwood, 1959) and, to a lesser degree, *H. empodisma* and *H. michaeli* (see Greenwood, 1960 and 1962 for the species respectively).

From *H. cronus*, it is differentiated by its dental morphology and its longer lower jaw.

From *H. empodisma*, *H. apogonoides* differs in its longer lower jaw (45·0–51·0, M = 47·9 per cent of head, *cf.* 39·1–48·7, M = 43·9%), dental morphology (strongly *cf.* gently curved teeth), broader interorbital (27·5–31·0, M = 29·5% head, *cf.* 20·6–28·6, M = 24·3), broader snout, and noticeably wider dentigerous surface on the lower pharyngeal bone($1\frac{1}{5}$–$1\frac{1}{4}$ times as broad as long, *cf.* longer than broad).

Haplochromis apogonoides differs from *H. michaeli* in dental morphology (see above), in its slightly deeper body, shallower preorbital, broader interorbital, markedly broader snout, and deeper cheek (27·8–31·0, M = 29·2% of head, *cf.* 22·9–27·7, M = 25·8%). The lower pharyngeal bone is similar in both species, but the teeth in *H. apogonoides* are stouter.

The marked similarity between the outer jaw teeth of *H. apognoides* and those in species of the *H. sauvagei* complex (which includes *H. xenognathus*, a species not mentioned above because of its distinctive jaw morphology, tooth pattern, and head shape) suggests that *H. apogonoides* might be an off-shoot from this species group. Unfortunately, nothing is known about the feeding habits of this species; all members of the *H. sauvagei* group are snail-eaters with the unusual habit of removing the snail from its shell before ingesting it. The large mouth and not especially strong jaws of *H. apogonoides*, do not, however, suggest similar feeding methods; rather, these characters indicate piscivorous habits.

Study material and distribution records

Museum and Reg. No.	Locality	Collector
	UGANDA	
B.M. (N.H.) 1966.2.21.3 (Holotype)	Ekunu Bay	E.A.F.R.O.
B.M. (N.H.) 1966.3.9.238–242	Ekunu Bay	E.A.F.R.O.
	LAKE VICTORIA	
B.M. (N.H.) 1966.3.9.236–237	Locality unknown . . .	E.A.F.R.O.

DISCUSSION

Phylogeny

In an earlier paper (Greenwood, 1962) I outlined the various morphological trends shown by the piscivorous species, and suggested a possible ancestral morphotype (represented today by *H. brownae*) from which the different lines could have evolved. Also in that paper I indicated two major, and two minor, possibly phyletic groups of fish-eating predators. Additional information provided by the species described above does not affect the suggested trends, but does alter the phyletic picture. It now seems likely that there are three major phyletic lines, and probably three minor ones as well.

As mentioned before (Greenwood, *op. cit.*), possible phyletic lines amongst piscivorous species are less readily detected and defined than those of other trophic groups. In these latter there are dental as well as somatic characters which may be used for this purpose, but amongst the piscivores (at least when adult) the teeth are invariably unicuspid and of a very similar form. The principal " group " characters in these fishes are neurocranial shape, and body form ; the latter character often shows a greater or lesser degree of intergroup convergence. Using these two character complexes, I at first recognized two species aggregates, the " *serranus* " group, and the " *mento-macrognathus* " group. The former comprises the supposedly more generalized, broad-headed and deep-bodied species, and the latter group the more specialized, slender-bodied forms.

Information obtained from the species described in this paper suggests that my " *mento-macrognathus* " group consists of two groups, neither of which is as readily defined as the " *serranus* " group, but both being easily distinguished from that group.

One of the minor groups (that of *H. percoides*, *H. flavipinnis* and *H. cavifrons*) is now thought to be polyphyletic (see p. 113).

For convenience the groups will be referred to by the trivial epithet of a constituent species, which species, however, is not necessarily to be considered a " typical " member of the group. Indeed it is often difficult to determine just what a " typical " species would be ; at the most, the nominate species of a group is representative of a structural type found in three or four species of the group.

The three major groups are : (i) The " *serranus* " group, consisting of *H. serranus*, *H. victorianus*, *H. nyanzae*, *H. spekii*, *H. maculipinna*, *H. boops*, *H. thuragnathus* and *H. pachycephalus :* morphologically, this is a relatively homogeneous group (but, see also p. 110).

(ii) The " *altigenis* " group, comprising *H. guiarti*, *H. bayoni*, *H. dentex*, *H. pseudopellegrini*, *H. altigenis*, *H. pellegrini* and *H. dichrourus* ; a number of subgroups (some monotypic) can be recognized, and are discussed later.

(iii) The " *prognathus* " group, comprising *H. paraguiarti*, *H. acidens*, *H. prognathus*, *H. bartoni*, *H. estor*, *H. gowersi*, *H. mento*, *H. mandibularis*, *H. macrognathus*, *H. longirostris* and *H. argenteus*. This, the largest species aggregate shows several intragroup trends of which the most distinctive are the *H. longirostris*—*H. argenteus*, and the *H. mandibularis*—*H. macrognathus* subgroups.

Members of the " *serranus* " group differ from those of the other two groups in having shorter snouts* (one species out of seven with the snout $>$ 36 per cent of head length, *cf.* fourteen species out of eighteen), deeper bodies (one species out of seven with the body depth $<$ 36 per cent of standard length, *cf.* seventeen out of eighteen), and broader heads (no species with the interorbital width $<$ 22·6 per cent of head, *cf.* thirteen out of eighteen species.) Osteologically, the group is character-

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* The figures given are derived from those for the mean value of a particular character in species of the groups under consideration.

ized by having a neurocranial shape nearest that of the generalized skull (see Greenwood, 1962), but with the preotic part elongate. The dorsal skull roof is straight and slopes fairly steeply, is broad both interorbitally and across the otic region, and the supraoccipital crest is high and presents a substantial area for muscle insertion (see fig. 25 in Greenwood, *op. cit.*).

The " *serranus* " group could have evolved directly from an *H. brownae*-like ancestor, the principal morphological changes being an increase in adult size, and those alterations in neurocranial proportions already mentioned. Within the group, the most differentiated species are *H. boops*, *H. thuragnathus* and *H. pachycephalus*, all three being confined to deep water (see pp. 49, 50 and 41). *Haplochromis boops* and *H. thuragnathus* were apparently derived from an *H. maculipinna*-like ancestor, whilst *H. pachycephalus* seems to show greater affinity with the *H. serranus—H. spekii* level of organization. *Haplochromis maculipinna* is also essentially of this affinity, but has markedly larger eyes. In turn, *H. serranus* is clearly derived from an *H. brownae*-like stem.

The " *altigenis* " and " *prognathus* " groups probably evolved from an *H. guiarti*-like ancestor or ancestors, the latter species also showing affinities with *H. brownae*. Although both the " *altigenis* " and " *prognathus* " groups have included species with a relatively deep body, the main trend shown by both groups is towards a slender, somewhat compressed body-form and a correlated head shape. It is difficult to characterize these two groups, particularly their more basic members. The most trenchant group characters are probably in neurocranial form. In lateral view there is little to differentiate the skull form in the two groups ; both have the preorbital part relatively more elongate than in the " *serranus* "-type skull, the dorsal profile slopes upward at a rather slight angle (as compared with the angle in skulls of the " *serranus* " group), and the supraoccipital crest is relatively low. (These generalizations must, however, be modified somewhat for those species which seem to be structurally basal for the groups [*H. guiarti* and *H. pseudopellegrini* for the " *altigenis* " group, and *H. paraguiarti* and *H. acidens* for the " *prognathus* " group]. In these species the preorbital face is less protracted and consequently [since relative neurocranial depth varies little amongst all members of both groups] the dorsal skull roof slopes more steeply and the supraoccipital crest is higher and has a fairly extensive area). However, when the neurocranium is viewed dorsally, a difference between the groups (including their basal species) is apparent (see text-fig. 24). In members of the " *altigenis* " group, the otic region is relatively broader than in those of the " *prognathus* " group so that the outline narrows more rapidly (from a point immediately behind the orbit) than in " *prognathus* " skulls. In these the outline is that of a narrow wedge with the margins closing gradually from a point further behind the orbits. In supposedly basal members of both groups, the otic region is of about equal relative breadth but basal " *prognathus* " members nevertheless have a more gradual medial inclination of the lateral margins. Furthermore, in these species the dorsal skull profile is straighter than in the most basic " *altigenis* " group member, *H. guiarti*. Indeed, in most members of the " *altigenis* " group the profile is more curved than in species of the " *prognathus* " group.

Reasons for considering *H. guiarti* as a basic morphotype in the radiations of

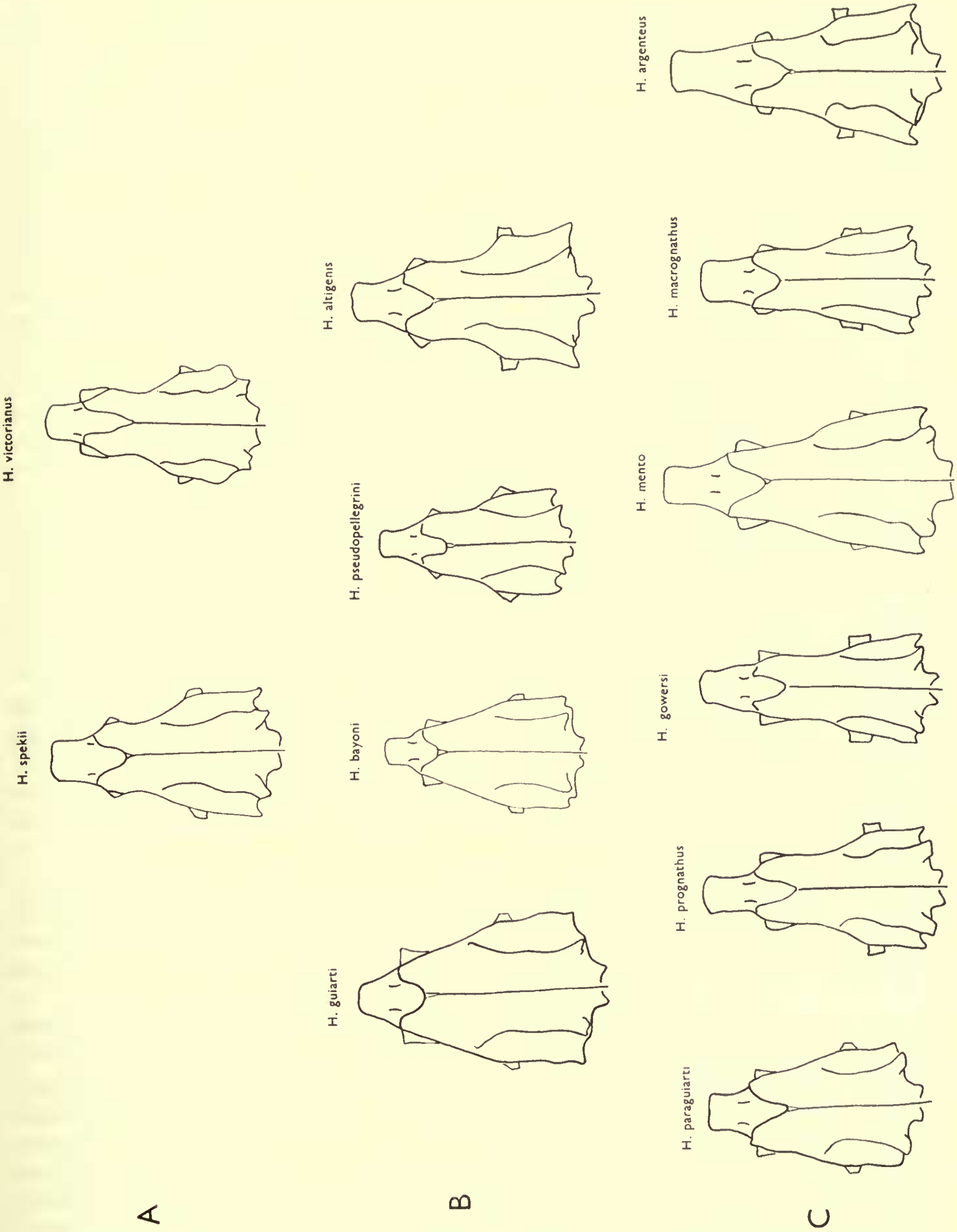

FIG. 24. Outlines of the dorsicranium in species of: line A, the " *serranus*-group ", line B, the " *altigenis*-group ", and line C, the " *prognathus*-group".

predatory piscivores have been discussed already (see Greenwood, 1962). Starting from a species similar to *H. guiarti*, the principal morphological changes seen amongst species of the "*altigenis*" group involve relative elongation of the preorbital face, a slight decrease in skull height (especially in the otic region) and a consequent flattening in the slope of the dorsal skull profile. In these respects *H. bayoni* represents a fairly marked departure from the basic "*guiarti*" skull form, but one less marked than that shown by *H. dentex*, *H. altigenis* or *H. pellegrini*, particularly the latter (see fig. 25 in Greenwood, 1962). A link between these forms is provided by the skull of *H. pseudopellegrini* which is intermediate between the "*bayoni*" and "*altigenis*" types. There is not a great deal of difference in body form or jaw morphology among members of the "*altigenis*" group. Perhaps the most extreme member is *H. altigenis* itself, a species with the deepest head and consequently the largest mouth. *Haplochromis pellegrini* is, because of its small adult size and relatively small mouth, atypical for the group.

There is far greater variation in body form and cranial morphology within the "*prognathus*" group. Here the basic species, *H. paraguiarti* and *H. acidens*, are morphologically similar to *H. bayoni* of the "*altigenis*" group and could be derived either from a "*bayoni*" or a "*guiarti*"-like ancestor. *Haplochromis acidens* is, of course, peculiar in that despite its predatory facies, it is apparently a phytophage (see p. 76). *Haplochromis prognathus* and *H. bartoni* are, in most respects, very similar to one another and represent the next morphological step in the evolution of such species as *H. longirostris* and *H. mandibularis* from a "*paraguiarti*"-like stem. That is to say, the neurocranium clearly shows narrowing and elongation, and there is a related refinement of body proportions. *Haplochromis estor* and *H. gowersi* continue this trend with, in addition, the development of a more oblique angle to the jaws, and in *H. gowersi* a deepening of the cheek which contributes to a larger buccal cavity. *Haplochromis mento* probably evolved from a "*prognathus*"-like ancestor, and shows many of the trends exhibited by *H. gowersi* and *H. estor*. However, in this species the mouth is almost horizontal, and the neurocranium is somewhat nearer that of *H. prognathus*.

Also apparently stemming from a "*prognathus*"-like ancestor is *H. mandibularis*. Here the trend is towards further narrowing of the skull, deepening of the cheek, increased obliquity of the jaws and lengthening of the lower jaw. This trend culminates in *H. macrognathus* (see Greenwood, 1962, pp. 180 and 186), a species which could well be a direct descendant of *H. mandibularis*.

A third derivative from a "*prognathus*" or "*bartoni*"-like ancestor is *H. longirostris*. In this line there has been little change in neurocranial shape but there is a marked increase in jaw obliquity (much greater, too, than in the "*mandibularis*"-"*macrognathus*" line), and a marked refinement in body proportions which results in one of the most slender bodies found amongst Lake Victoria *Haplochromis* species. These characters are shared by *H. argenteus*, although the elongate body-form seems less obvious in that species. *Haplochromis argenteus* could be derived either from a "*longirostris*"-like stem, or perhaps directly from a "*prognathus*"-like ancestor.

Thus, the "*prognathus*" group seems to show at least three radiations from a basal "*prognathus*"–"*bartoni*" stem, *viz.* the *H. estor*, *H. gowersi*, *H. mento* sub-group, and the *H. mandibularis–H. macrognathus*, and *H. longirostris–H. argenteus* species pairs (but see above for possible reservations about the last named pair). It seems reasonable to assume that the *H. prognathus* level of organization was derived from a level similar to that shown by the extant species *H. paraguiarti*. The relationships of that species are, however, less clear-cut. As was mentioned above, *H. paraguiarti* shows several structural affinities with *H. bayoni*, a species probably derived from an *H. guiarti*-like ancestor. But, it is difficult to overrule the possibility that *H. paraguiarti* evolved independently from an *H. brownae*-like stem. (The status of *H. brownae* in relation to the piscivorous predators is discussed in Greenwood, 1962).

Two species, *H. plagiostoma* and *H. xenostoma*, have not been included in the discussion so far. Both are characterized by having the mouth set at a very steep angle to the horizontal (*ca.* 40°–50°) ; *H. plagiostoma* is further characterized by its obliquely truncate caudal fin, and *H. xenostoma* by its pronounced prognathism. Because of these characters, especially the oblique jaws, neither species shows any obvious superficial similarity with members of the groups discussed above. The neurocranium of *H. plagiostoma* is of the "*serranus*" type (see also Greenwood, 1962) but also shows certain "*guiarti*"-like features. Thus, on this character complex *H. plagiostoma* could either be associated with the "*serranus*" group or be looked upon as an isolated offshoot of the "*altigenis*" group arising from an ancestor near the stem of that complex. In either eventuality, *H. plagiostoma* is not linked with the basal group by any extant, structurally intermediate species.

Haplochromis xenostoma, both in its overall organization and in its neurocranial form, seems to represent a further development from a "*plagiostoma*" stem. The chief trend involves an increase in adult size, and a relative enlargement of the mouth and jaws. The neurocranium of *H. xenostoma* reflects these changes, especially in the longer preorbital region ; it is thus essentially a "*serranus*" group neurocranium. From the available evidence it is impossible to determine whether *H. plagiostoma* and *H. xenostoma* are part of the same phyletic lineage or whether the two species are end-points of parallel evolution from "*guiarti*" and "*serranus*"-like stems respectively.

The two smaller species complexes, the *H. michaeli*, *H. martini*, *H. squamulatus* group and the *H. percoides*, *H. flavipinnis*, *H. cavifrons* group, will now be considered.

The relationships of *H. michaeli* and *H. martini* are discussed in my paper of 1962, and there is nothing further to add. *Haplochromis squamulatus* is included with these species because of its several similarities with *H. martini*, similarities which include a basically similar coloration of a type not otherwise found in species of the Lake Victoria *Haplochromis* flock. In the "*michaeli*" group, the relationship between *H. martini* and *H. squamulatus* seems to be closer and more direct than that between either species and *H. michaeli* (see also Greenwood, 1960, pp. 245–8 ; *idem*, 1962, p. 206, and p. 91 above).

When discussing the relationships of the *H. percoides–H. cavifrons* group (Greenwood, 1962), I suggested that *H. percoides* could have evolved from an *H. pellegrini*-like stem, and that *H. flavipinnis* was a derivative of an *H. percoides*-like ancestor. Also in that paper I noted the less certain relationships of *H. cavifrons*, but considered it to be part of the *H. percoides* phyletic line. On revising this complex, I began to doubt my earlier conclusions about the affinities of *H. cavifrons*, which now seems to have greater relationship with the " *serranus* " group. This review provided no evidence to negative my conclusions about the interrelationships of *H. percoides* and *H. flavipinnis*, or the association of *H. percoides* with an *H. pellegrini*-like ancestor. However, I am not at all certain about the validity of my previous suggestion that the neurocrania of *H. percoides* and *H. flavipinnis* show affinity with those of *H. bartoni* and *H. longirostris* (i.e. with the " *prognathus* " group as it is now defined). With a better appreciation of neurocranial form in the piscivores as a whole, I now think that the skull of *H. percoides* is basically an " *altigenis* " group one, as is the skull of *H. pellegrini*.

Similar re-evaluation leads me to think that the syncranial organization and form shown by *H. cavifrons* links that species more closely with the " *serranus* " group than with the " *altigenis* " group and its *H. percoides*-like off-shoots. The freckled coloration of *H. cavifrons* remains unique (Greenwood, 1962), and nothing approaching it is seen in the " *serranus* " group. If *H. cavifrons* is a " *serranus* "-group derivative, then it stands in the same relationship to that group as does *H. plagiostoma*, namely as an isolated off-shoot without any extant intermediates bridging the gap.

Thus, the *H. percoides–H. cavifrons* " group ", although a valid one on grounds of general similarity between the constituent species, is probably polyphyletic in origin.

Because so little material or information is available on three species described above (*H. tridens*, *H. orthostoma*, and *H. parorthostoma*), they cannot as yet be included in a discussion on phylogeny. *Haplochromis tridens* does not seem to be related to any of the piscivorous species groups ; its affinities probably lie with the complex of small, bottom-living species which form the bulk of trawl catches in sheltered, mud-bottomed areas of the lake. *Haplochromis orthostoma* and *H. parothostoma* are closely related to one another but cannot readily be associated with any other species.

Leaving for the moment those species which as adults feed on post-larval fishes, consideration will be given to species which prey on larval and embryo fishes, the paedophagous species. Only one paedophage, *H. barbarae*, is described in this paper ; the others are dealt with in an earlier publication (Greenwood, 1959).

Haplochromis barbarae resembles small specimens of *H. guiarti* and adults of *H. brownae*, and does not show any close similarity in body form, jaw morphology or dentition with other paedophagous species; unfortunately it has not been possible to study its osteology in detail. The probable phylogeny of the larval and embryo fish eating species was discussed in the paper cited above ; the conclusion reached was that the group had a polyphyletic origin. Little more can be added to these thoughts, except to reconsider the possible relationships existing between *H. parvidens* and *H. acidens* (previously misidentified as *H. nigrescens*; see above, p. 73). The morphology of the lower jaw in *H. parvidens* differs considerably from that of *H. acidens* (as does the diet, paedophage *cf.* herbivore) ; but, in other syncranial characters, and in body-form, the species are very similar. In these latter characters the two species are more similar than are *H. microdon* and *H. cryptodon*, the only known paedophages showing a morphotype which could be ancestral to that of the "*parvidens*" level. *Haplochromis cryptodon* could have evolved from an *H. brownae*-like stem (possibly one like *H. barbarae* which had already adopted paedophagous habits?), the chief morphological changes involving the dentition (reduction), jaw form (to give greater distensibility) and a differential growth of the preorbital neurocranium (also leading to greater jaw motility). The changes in neurocranial form would lead to a skull essentially like that found in basal species of the "*altigenis*" and "*prognathus*" groups, in other words one like that in *H. acidens*. Thus, the origin of the "*parvidens*" structural grade is equivocal.

Reconsidering the relationship of this grade (as represented by *H. cryptodon*, *H. parvidens* and *H. microdon*) with the other distensibly-mouthed grade of paedophages (represented by *H. obesus* and *H. maxillaris*), I can find, as before, few reasons to support a close phyletic linkage between them. Osteologically neither *H. obesus* nor *H. maxillaris* has a dentary like that occurring in the *H. parvidens* group, nor in the case of *H. obesus* is its form one from which a "*parvidens*" type might evolve. The neurocranium of *H. obesus* is most unlike that of the "*parvidens*" group, but that of *H. maxillaris* is virtually identical with the skull of *H. cryptodon*. The character which most clearly distinguishes these two species from any member of the "*parvidens*" group is the occurrence of teeth in which the crowns are curved labially (and not buccally as is usual in unicuspid teeth). This dental character is so marked, and restricted to these two species, that I am inclined to give it considerable weight when speculating on phylogenies, particularly since this tooth-form seems to have no adaptive significance. If the peculiar teeth in *H. maxillaris* and *H. obesus* do indicate a fundamental relationship between the species, then their syncranial differences would suggest an independent origin from a common stem, possibly a form like *H. cronus* (see Greenwood, 1959). Dentally, and also in its general level of organization, *H. cronus* is like those generalized *Haplochromis* species that attain a larger adult size than most members of that group ; it could be derived from an *H. empodisma*-like stem (see Greenwood, 1960).

Natural History

Only broad generalizations can be made about the natural history of the piscivorous predators. To date, seventy-nine species of Lake Victoria *Haplochromis* (and related monotypic genera) have been revised. Of these, forty-two species can be classed as piscivores, thirty-four species preying on free-swimming fishes, and eight species on cichlid embryos and larvae presumably taken from the mouths of parent fishes. Anticipating results still to be obtained from those species as yet unanalyzed, it seems probable that the number of non-piscivorous species will be increased substantially. I suspect that ultimately the number of piscivorous species will be about forty per cent of the total. These figures apply to sub-adult and adult members of the species only since no data are available on the feeding habits of younger stages. The same restrictions apply to considerations on habitat preferences among the piscivores.

Piscivorous species have been found in all the localities so far sampled, but much of the deeper water in Lake Victoria remains unexplored, especially at the levels occupied by bathypelagic species. In order to give a general picture of habitats in the lake, these can be divided, rather crudely, into three types : (i) sheltered areas such as bays and the smaller gulfs. (ii) Exposed areas, especially wave-washed beaches. (iii) Relatively undisturbed, open, off-shore waters (undisturbed that is, relative to the rather turbulent conditions prevailing over exposed beaches), not enclosed in gulfs or bays. Such a subdivision is, in many respects, unsatisfactory because conditions like those in habitat (iii) do occur in the larger gulfs and bays.

More species are found in sheltered areas (habitat [i]) than in the other two habitats ; 23 species have been recorded frequently in habitat (i), 14 from habitat (ii), and 15 from habitat (iii), with, in the habitats respectively, 2, 3, and 1 species occurring infrequently. However, these various species are by no means confined to a particular habitat. For example, 11 species were found in both sheltered and exposed areas, 9 in sheltered and off-shore habitats (3 of these species also occurring over beaches) ; only 6 species are apparently confined to sheltered areas. Two species occur both over beaches and in the quieter off-shore areas, and only 4 are apparently confined to the latter habitat (but 3 of these species are known only from deep water). The nature of the substrate seems to exert a less restricting influence on the piscivores than on members of other trophic groups. Twenty-four species are recorded as occurring over hard substrata (sand, shingle or rock), and 20 over a soft substrate (organic mud) ; 10 of these species are found over both kinds of substrate, 6 are thought to be confined to a soft bottom, and 13 to a hard substrate.

The eight strictly paedophagous species (see Greenwood, 1959, and p. 114 above) are not included in the analysis above. These species appear to be rather more restricted in their distribution, particularly from the viewpoint of depth range. It seems that the paedophages are confined to the littoral and immediately sublittoral zone, and are probably restricted to sheltered bays and exposed beaches.

The depth range of the other 34 piscivores is, in general, confined to water less than 60 ft. deep (with of course, the exception of *H. boops*, *H. pachycephalus*, *H. thuragnathus* and *H. dichrourus* which have been caught in water about 120 ft. deep). Most species have a wide range within these depth limits, and few if any are restricted to purely littoral areas. However, it must be emphasized that this picture may be unduly biased by sampling limitations. The horizontal distribution of the species has not been studied critically ; in water less than 20 feet deep, the spatial distribution of piscivores caught in nets set to cover about the first five feet of water below the surface, and the five feet above the bottom, does not show any obvious horizontal stratification of the particular species. But, these observations were not tested statistically.

From the relatively few gut analyses available it would seem that the majority of piscivores prey on other *Haplochromis* species, and to a much lesser extent on small cyprinid fishes (especially *Engraulicypris argenteus*). Some species have a mixed insect-fish diet, and there are several records of otherwise exclusively piscivorous species eating insects when these are periodically and suddenly super-abundant, as for instance after a heavy termite hatch. The paedophagous species appear to feed mostly on cichlid embryos and larvae (it is presumed those of *Haplochromis* species), but insects are also recorded from the gut contents of these species.

Information on the breeding habits of piscivores is almost non-existent ; in those cases where some data are available, the species are known to be female mouth brooders. The turbidity of the water in most parts of Lake Victoria has precluded field observations on the actual spawning sites of both predators and prey alike.

There has not yet been enough collecting on a lake-wide basis to establish whether or not any of the fish-eating species has a geographically restricted distribution. For eight species this possibility can definitely be overruled, (and in ten others it seems very unlikely) but for sixteen species there are suggestions of geographical restriction because they have not been caught in some regions where, on the basis of habitat and niche suitability, they should be present.

SUMMARY

(1) Ten species are redescribed on the basis of new material.

(2) Nine new species (*H. pachycephalus, H. boops, H. thuragnathus, H. pseudopellegrini, H. paraguiarti, H. acidens, H. barbarae, H. parorthostoma* and *H. apogonoides*) are described.

(3) Although all these species have a general facies and dentition usually associated with piscivorous habits, some do not belong to this trophic group ; one species (*H. acidens*) is apparently herbivorous.

(4) The possible phyletic interrelationships of the piscivorous species are discussed. Three major morphological groups can be detected, at least on the basis of their more extreme members, but the boundaries are ill-defined. Some minor groups are also considered, as are the larval and embryo fish-eating species groups.

(5) Broad summaries of the natural history of piscivorous species are given.

(6) The holotype of *Astatotilapia nigrescens* Pellegrin is redescribed and its possible synonymy discussed.

ACKNOWLEDGEMENTS

I am deeply indebted to many people for their assistance in preparing this paper.

To my colleagues Mr. A. C. Wheeler and Dr. E. Trewavas are due my thanks for, respectively, providing numerous and excellent radiographs, and for many profitable discussions.

Through the cooperation of Dr. M. Blanc of the Paris Museum, I have been able to examine Pellegrin's type specimens and thus to settle several problems. Dr. Paul Kahsbauer of the Vienna Museum has graciously lent me Lohberger's type material ; I am deeply indebted to him for this privilege.

In east Africa, Dr. M. Gee and Mr. R. Welcomme of E.A.F.F.R.O. aided my studies by proving additional material and field observations ; material collected by the Uganda Fisheries Department has provided many specimens from localities which I was unable to sample personally. The cooperation of E.A.F.F.R.O. and the Uganda Fisheries Department is warmly appreciated.

APPENDIX

The disputed identity of *Astatotilapia nigrescens* Pellegrin, 1909, (*Bull. Soc. Zool. France*, **34**, 157) was mentioned on page 73. Boulenger (1915) synonymized this species with *Haplochromis percoides* Blgr. 1906. Regan (1922), however, resurrected the species as *Haplochromis nigrescens,* and included in his redescription a number of specimens which I have placed in a new species, *H. acidens*. Pellegrin's figure of *A. nigrescens* is misleading and does not convey an accurate impression of the holotype and unique specimen (Paris Museum, number 09–508).

Recently, I examined this specimen, an immature male 71 mm. standard length, collected by Alluaud from the Kavirondo Gulf, Kenya. It does not agree closely with any other specimens I have handled, but is does show affinity with both *H. percoides* Blgr., 1906 and *H. flavipinnis* (Blg.), 1906, especially the latter.

Before considering its identity further, a redescription of the holotype will be given.

	mm.	Proportional percentage
Standard length	71·0	
Depth of body	24·0	33·8 standard length
Length of head	26·0	36·6 standard length
Depth of preorbital	4·3	16·5 head length
Width of interorbital	6·0	23·1 head length
Length of snout	8·0	30·8 head length
Diameter of eye	7·0	27·0 head length
Depth of cheek	6·5	25·0 head length
Length of lower jaw	12·0	46·2 head length
Length of caudal peduncle	13·0	18·3 standard length
Length of pectoral fin	18·0	25·3 standard length

Caudal peduncle 1·4 times as long as deep.

Lower jaw slightly oblique and very slightly projecting ; twice as long as broad. Posterior tip of the maxilla almost reaching the vertical through the anterior orbital margin.

Gill rakers : moderately stout, 9 on the lower part of the first gill arch.

Scales : ctenoid ; lateral line with 31 scales, cheek with 4 rows (the rows short, so that the anterior part of the cheek is naked). Seven scales between the upper lateral line and the dorsal fin origin ; 7 between the pectoral and pelvic fin bases. Chest, belly and nuchal scales small.

Teeth : in the outer row of both jaws relatively slender, slightly curved ; about 50 in the upper jaw. Inner teeth tricuspid or weakly tricuspid, arranged in 2 and 1 rows in the upper and lower jaw respectively.

Coloration. The preserved colour pattern (in shades of brown) closely resembles that of *H. percoides* and *H. flavipinnis* (see Greenwood, 1962). The dorsal fin is marbled, and the caudal both marbled and maculate ; the pelvics are dark.

DISCUSSION : In its general facies, and particularly its head shape, the holotype of *A. nigrescens* resembles both *H. percoides* and *H. flavipinnis,* especially the former because the angle of the mouth is less oblique than in most specimens of *H. flavipinnis.* However, when morphometric characters are considered a number of differences between *H. percoides* and *A. nigrescens* holotype are apparent. In six characters (body depth, preorbital depth, interorbital width, snout length, eye diameter, and caudal peduncle length) the values fall outside the known range for *H. percoides*, and the lower jaw is relatively longer than in specimens of *H. percoides* of a comparable size.

There is greater correspondence between these characters in *A. nigrescens* and *H. flavipinnis*, since only two (the shallower preorbital and larger eye) fall outside the range for *H. flavipinnis*, but there is a greater difference in head shape.

Thus, *A. nigrescens* could be an aberrant specimen of either *H. flavipinnis* (differing especially in head shape) or *H. percoides* (numerous morphometric differences).

For the time being, however, I do not think that *A. nigrescens* can be formally synonymized with either species. I would prefer to recognize it as the purely nominal species *Haplochromis nigrescens* (Pellegrin) until more is known about the range of variation in small specimens of *H. flavipinnis*, the species I think it most closely resembles.

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